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CORRELATION OF CURRENTS WITH THE DISTRIBUTION OF ADULT *DAPHNIA* IN LAKE MENDOTA¹

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ABSTRACT

Simultaneous observations of current pattern and distribution of *Daphnia pulex* indicate that in Lake Mendota this zooplankter is concentrated by wind-induced convergence. Theoretical examination of this hypothesis yields results which compare favorably with observations.

In general it has been assumed that inland lakes are horizontally homogeneous. As a corollary, the lateral variation of plankton at a specified depth has been regarded as approximately random. Ricker (1938a, b) found that the horizontal variation in zooplankton in Cultus Lake, B. C., exceeded slightly the random variation. In Lake Nipissing, Ontario, Langford (1938) sampled 10 stations in a line and concluded that there was no trend in the numbers of *Daphnia*.

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He found them randomly distributed at the surface and nearly so at one meter. On the other hand, Verduin (1951) found two distinct populations of diatoms in the western end of Lake Erie which were apparently associated with the hydrography of the region. However, the physical dimensions of Lake Erie place it in a different class from Cultus or Nipissing.

In Lake Mendota we have found large horizontal variations of zooplankton. This is evident in Figs. 3, 6, 9-12. We shall show how the zooplankton is mechanically concentrated and transported from one location to another.

This sort of problem is not new to oceanographers. Damas (1905) considered the problem for the Norwegian Sea, and Sømme (1934) re-examined this area and gave a more adequate explanation of the maintenance and transport of calanoid populations as related to the movements of the water in this Sea. More recently Redfield (1939, 1941) and Redfield and Beale (1940) described the relation of the Gulf of Maine circulation to an immigrant population of *Limacina retroversa*, the chaetognaths in the Gulf, and to a calanoid community existing there with a limited connection to the open ocean. Russell (1935, 1939) has used certain planktonic species as indicators of water movements in the North Sea. Sverdrup and Allen (1939) showed the relationship of diatom distribution to the water masses and currents off the California Coast. One of the most recent contributors to this problem is Carruthers (1951). Numerous other studies could be cited to illustrate the point.

Methods. Preliminary sampling indicated the existence of considerable horizontal variation of the zooplankton in Lake Mendota. The variation in samples from one location to another frequently ranged through several orders of magnitude and was greater than the variation among replicate samples at one station. By variation we mean gross changes rather than microvariation due to foamlines (Stommel, 1949). The mechanism or mechanisms which produce and maintain these variations were then investigated.

An experiment which shows the movement and aggregation of zooplankton under the influence of wind-driven currents was conducted in University Bay during the spring of 1952. This Bay was used for this particular experiment for three reasons: it is bounded on three sides by land, its current pattern was better understood than that of any other region of Lake Mendota, and its size was convenient for the planned experiment. The Bay was covered by a grid of 15 stations, each of which was carefully fixed by a buoy. At the same time each day, for three days, the zooplankton was sampled and the

current was measured at all stations. Zooplankton samples, taken with the Clarke-Bumpus plankton sampler, averaged about 600 l each. Currents were measured by the drag method (Putnam, et al., 1949). The entire area could be covered in about three hours.

Daphnia pulex was the zooplankton used for the study. In early spring, before the Lake has stratified, *D. pulex* is most dense at about one meter. There is little or no diurnal vertical migration (Birge, 1895). From these data it was possible to construct one meter synoptic maps of *D. pulex* concentration, currents, and vertical velocity (Bryson and Suomi, 1952) for three consecutive days.

In this experiment, only large adult *Daphnia* representing the winter population were counted. This procedure automatically eliminated the factor of biological production. The death rate was not known, but no evidence of unusual mortality during this period was observed, as it was two weeks later.

Results. In Fig. 1 the current pattern at one meter for the first day of the experiment is shown by streamlines. The wind had been west and had changed to the north during that day's survey. Currents had a general southerly set and were relatively weak. The distribution of vertical velocities (Fig. 2) shows that upwelling was occurring in the center of the Bay while sinking was general along the south shore.

TABLE I.—WIND DATA, 1952

Date April	Prevailing Direction	Av. Velocity (mph)	Date May	Prevailing Direction	Av. Velocity (mph)
16	W	6.8	1	NW	6.5
17	W	9.5	2	ENE	9.8
18	WSW	8.7	3	SSW	6.1
19	WSW	5.9	4*	WSW	11.2
20	S	5.0	5*	W	14.0
21	SSE	12.0	6	NW	13.0
22*	NNW	11.5	7*	ESE	14.4
23*	ENE	16.0	8	NE	10.3
24*	NNE	9.8			

* Dates of plankton surveys.

Fig. 3 shows the distribution of *D. pulex* at one meter for the same day. Within the Bay the concentration varied from 9 to 380/m³. Such low densities indicated that most of the zooplankton had been swept out of the Bay by the preceding west winds. The concentration gradient was directed as expected, namely increasing toward the region of convergence, with the lowest values in the region of upwelling.

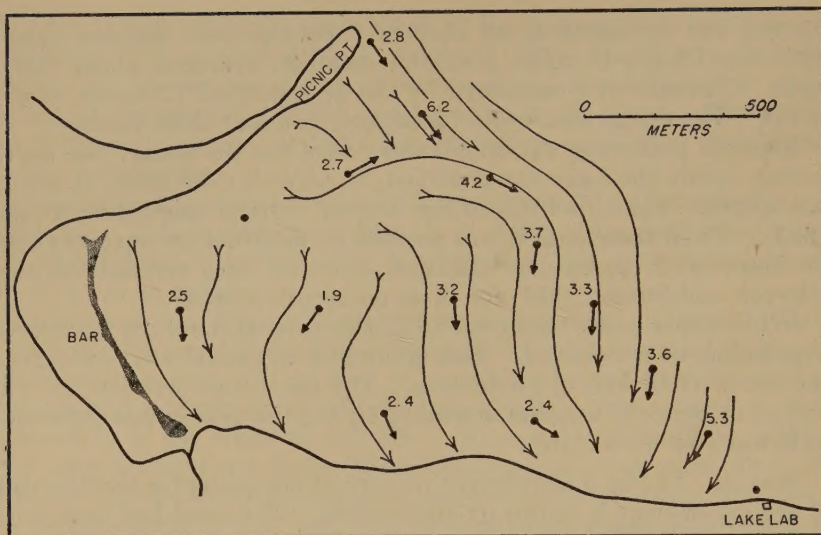


Figure 1. April 22, 1952. Current streamlines (spaced inversely proportional to velocity) for one meter level in University Bay; station values cm/sec.

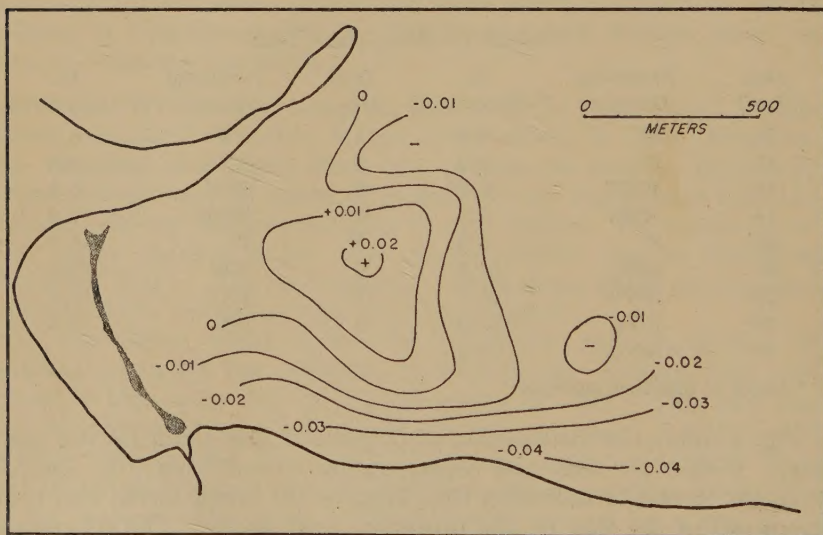


Figure 2. April 22, 1952. Vertical velocity distribution at one meter level in University Bay (cm/sec).

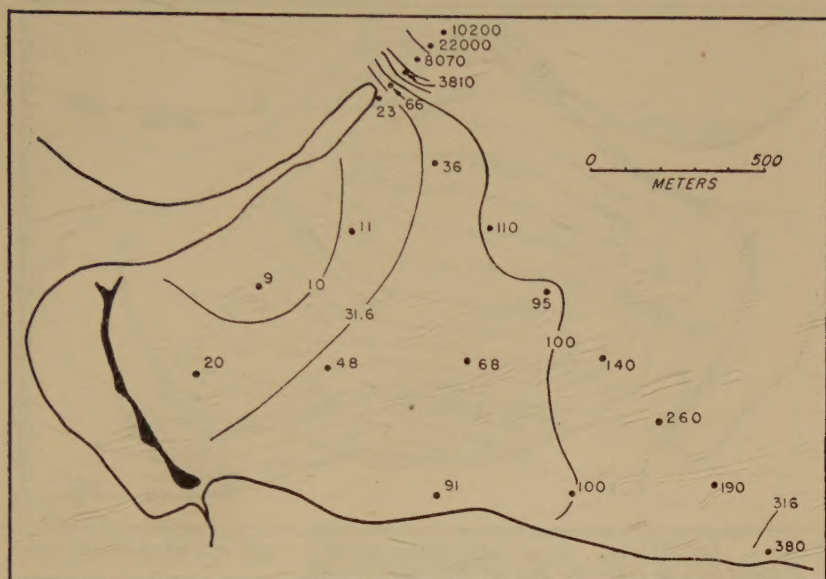


Figure 3. April 22, 1952. Distribution of *Daphnia pulex* adults at one meter in University Bay (no./m³; contours drawn on logarithmic scale).

After the organized survey was completed, reconnaissance to locate the main mass of plankton showed that it was situated off Picnic Point. Auxiliary stations were set up 50 yards apart and samples were taken at one meter. Here the gradient was extremely steep, and concentrations as high as 22,000/m³ were found. Unfortunately no hydrographic data are available for this region, but as will be shown later, convergence was probably occurring.

By the second day (Figs. 4 and 5) the current pattern had changed radically. The wind was from the east-northeast at 16 mph (Table I), and velocities of the currents were generally about twice those of the previous day. The flow was westerly throughout the entire Bay except near the bar at its head. Here the current was upwind, leading to high convergence values immediately out from this station and probably all along the bar. Some convergence was also occurring near the center of the Bay mouth. The effects of this change on the zooplankton distribution were striking but not entirely unexpected.

The *Daphnia* distribution for the second day (Fig. 6) shows that the mass of *Daphnia* off the Point moved into the Bay and was still concentrated with densities up to 15,000/m³. A second cell with a density of 1,000/m³ appeared near the center of the Bay mouth where convergence was occurring.

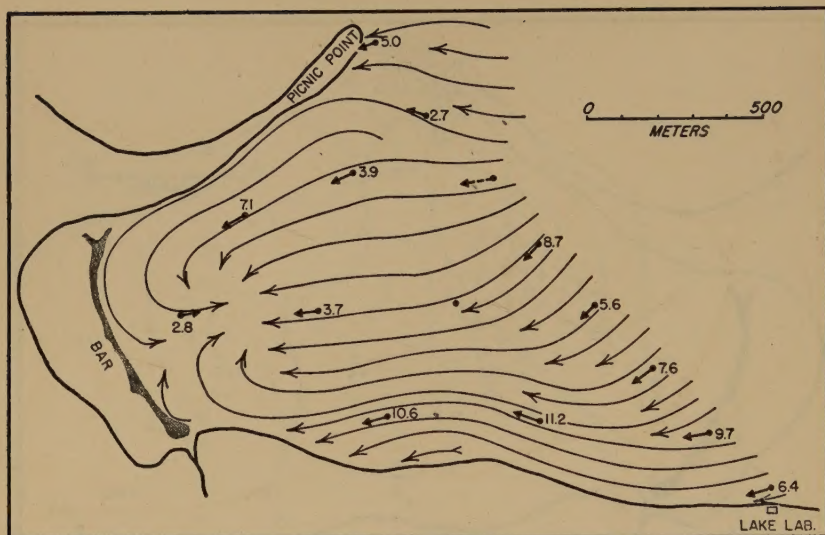


Figure 4. April 23, 1952. Current streamlines (spaced inversely proportional to velocity) for one meter level in University Bay; station values cm/sec.

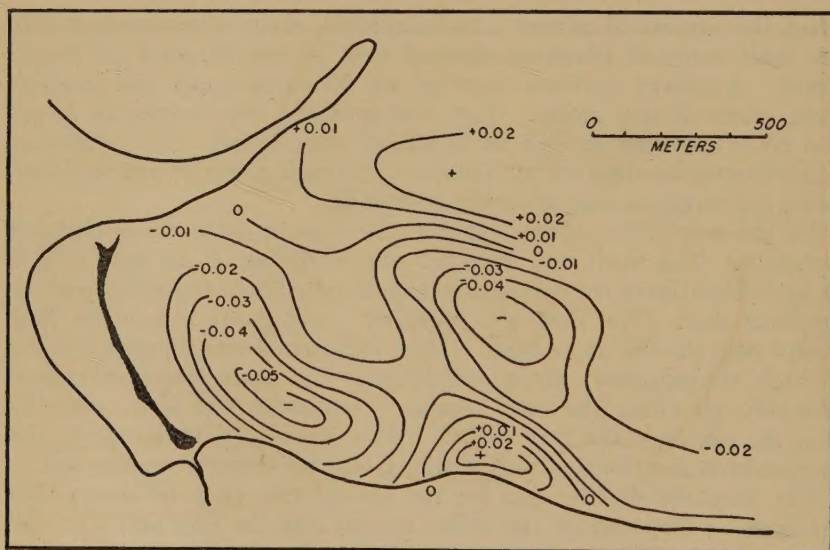


Figure 5. April 23, 1952. Vertical velocity distribution at one meter level in University Bay (cm/sec).

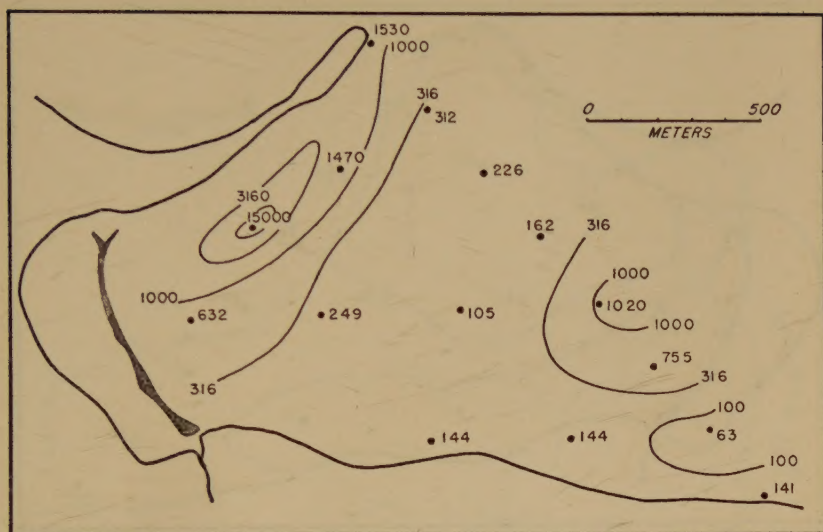


Figure 6. April 23, 1952. Distribution of *Daphnia pulex* adults at one meter in University Bay (no./m³; contours drawn on logarithmic scale).



Figure 7. April 24, 1952. Current streamlines (spaced inversely proportional to velocity) for one meter level in University Bay; station values cm/sec.

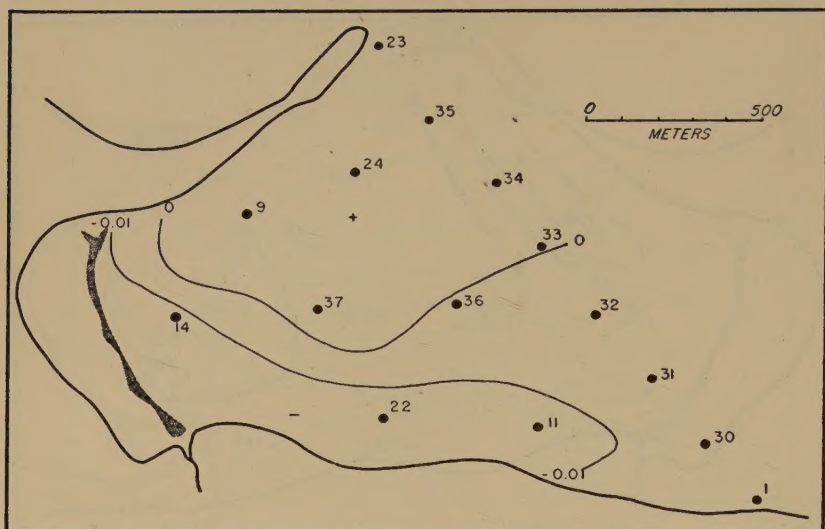


Figure 8. April 24, 1952. Vertical velocity distribution at one meter level in University Bay (cm/sec); values are station numbers for reference purposes.

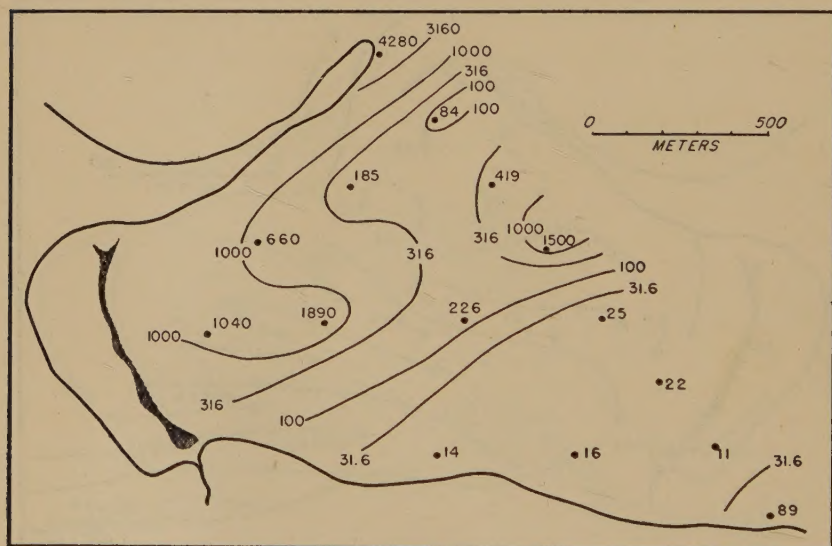


Figure 9. April 24, 1952. Distribution of *Daphnia pulex* adults at one meter in University Bay (no./m³; contours drawn on logarithmic scale).

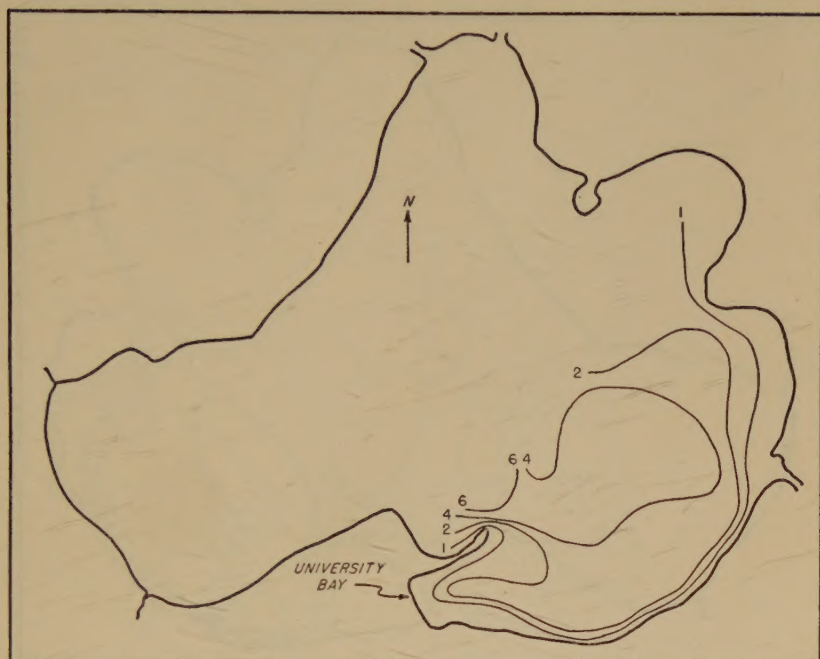


Figure 10. May 4, 1952. Distribution of *Daphnia pulex* adults in part of Lake Mendota by direct observation (values are no./sq. in. of viewer glass; see text).

By the third day (Figs. 7 and 8) the wind was north-northeast and had slackened to 10 mph; as a result the circulation pattern began to change. The general westerly drift persisted in the southern half of the Bay mouth but deteriorated somewhat in the northern half. Velocities decreased and the inflow along the Point held close to shore. Deep in the Bay the flow curved southward. Except along the southern shore, vertical velocities were practically zero.

The change of current pattern was reflected in the *Daphnia* distribution (Fig. 9). The heavy plankton concentration near the Point swung southward and began to disperse. Maximum concentrations decreased from 15,000 to less than 2,000/m³. There was a northward shift of the cell in the mouth of the Bay.

Although this experiment was terminated on the third day, more surveys of the *Daphnia* distribution were carried out May 4, 5, 7, and 8, but only a few samples were taken on the last day. This later series was made as follows: The glass plate of an underwater viewer was marked off in one-inch squares so that *D. pulex* could be observed



Figure 11. May 5, 1952. Distribution of *Daphnia pulex* adults in part of Lake Mendota by direct observation (values are no./sq. in. of viewer glass; see text).

directly. The winter individuals could be recognized immediately by their whitish color due to a microsporidial disease. There was no reason to believe that the incidence of this disease varied from one location to another. The number per square inch of viewer was estimated several times at each stop, and the results were plotted as shown in Figs. 10, 11, and 12. The authors do not intend to imply that this direct observation method is quantitatively comparable to sampling with the Clarke-Bumpus plankton sampler. However, direct observation gives the pattern of distribution over a large area whereas sampling yields detailed information over a limited area.

On May 4 (Fig. 10) a heavy concentration of *Daphnia* was observed off Picnic Point, and concentrations of four or more per square inch were noticed in the south central region of the Lake. A tongue of moderate concentration (2 per square inch) extended deep into University Bay (bottom center of map). By the next day, May 5, the west-southwest wind had shifted to due west and had increased in velocity (Table I), the great mass of *D. pulex* had reached the south shore, and the tongue in University Bay had moved out completely (Fig. 11). Concentration of the crustaceans had occurred, and it



Figure 12. May 7, 1952. Distribution of *Daphnia pulex* adults in part of Lake Mendota by direct observation (values are no./sq. in. of viewer glass; see text).

was estimated by direct observation that there were 10 per square inch. On May 6 the wind was from the northwest, but by the next day it was east-southeast at an average speed of 14 mph. This shift was quickly reflected in the distribution of *D. pulex* (Fig. 12). There were high concentrations off Picnic Point again, and deep in the Bay there was an extremely heavy concentration. In the central region of the Lake there were streaks of high concentration which alternated with bands of somewhat lower concentration. The streaks appeared to be associated with foamlines where there is generally convergence of the surface water. As shown in Fig. 12, the estimated values in and out of the streaks varied from 4 to 10 per square inch. On the same day the west end of the Lake had a relatively sparse population with only two cells of high concentration apparently trapped in the southwest corner. First evidence of a mortality of the winter population of *D. pulex* was observed this same day along the south shore at the west end of the Lake. The numbers of dead *Daphnia* were such that the bottom appeared whitish in depths of one to two meters along nearly one-half mile of shoreline.

On the following day, May 8, no general survey was made, but the plankton mass in University Bay was even more concentrated due to the northeast wind. Samples were taken with the Clarke-Bumpus sampler in this region and also in the center of the mouth of the Bay. Table II gives the results.

TABLE II.—*D. pulex* CONCENTRATION ON MAY 8, 1952

Station	Estimated No. per sq. in. of viewer by direct observation	Actual Nos. per m ³ by sampling at 0.5 to 1.0 m
Head of Bay	20+	2,000,000 (adults)
Mouth of Bay	0.05–0.1	15,000 (mostly juveniles)

Following examination of the hydrographic data it appeared likely that the accumulation of this tremendous mass of plankton was due to mechanical processes rather than to "swarming" of the animals themselves.

Theory. It is quite clear from this experiment as well as from other similar surveys that the concentration of *Daphnia* at a particular location may change by several orders of magnitude within 24 hours. In the light of the close correlation of the movements and aggregation of the zooplankters with the movements of the water, it seems reasonable that the explanation of the variations in concentration is related to the physical forces at work.

We have attempted to construct a mathematical model of the process which causes concentrations of *Daphnia* and other plankters to appear and move about the Lake. Naturally such a model is idealized and will have limits in its application, but up to the present it is the best explanation we have of the phenomena that do occur.

The theory is based on two assumptions:

1. It is assumed that the *Daphnia* do not exhibit purposeful horizontal motion. This is reasonable since pelagic animals can have no visual points of reference and must rely on thermal or chemical gradients to guide them in their lateral movements. In Lake Mendota horizontal temperature gradients may reach 1° C in 100 m, but usually they are less. It is doubtful if an animal as small as *D. pulex* (approximately 1 mm in length) could detect such a gradient.

2. The *Daphnia* orient themselves vertically by the light gradient from the surface. Vertical temperature and chemical gradients that occur later in the season only modify this orientation. This means that the *Daphnia* will tend to maintain their depth in spite of vertical currents in the Lake. Laboratory experiments have verified the fact that these animals are able to ascend or descend at a rate greater than most vertical current velocities observed in Lake Mendota, namely, 1 cm/sec or so.

With these two assumptions in mind, we shall take the equation for the distribution of a conservative variable in the sea as developed by Sverdrup, et al. (1946) and alter it so that it expresses the distribution of a known nonconservative variable, namely *D. pulex*:

$$\frac{\partial s}{\partial t} = \frac{\partial}{\partial x} \left(\frac{A_x}{\rho} \cdot \frac{\partial s}{\partial x} \right) + \frac{\partial}{\partial y} \left(\frac{A_y}{\rho} \cdot \frac{\partial s}{\partial y} \right) + \frac{\partial}{\partial z} \left(\frac{A_z}{\rho} \cdot \frac{\partial s}{\partial z} \right) - \left[\frac{\partial(s \cdot v_x)}{\partial x} + \frac{\partial(s \cdot v_y)}{\partial y} + \frac{\partial(s \cdot v_z)}{\partial z} \right], \quad (1)$$

where A is coefficient of eddy diffusivity, ρ the density, v the current velocity, and s the plankton concentration. This expression equates the local change of concentration to the effects of diffusion and the net flux of the variable (plankton concentration) in all three dimensions. Rewriting, we obtain

$$\frac{\partial s}{\partial t} = \text{Diffusion} - s \left(\frac{\partial v_x}{\partial x} + \frac{\partial v_y}{\partial y} + \frac{\partial v_z}{\partial z} \right) - v_x \frac{\partial s}{\partial x} - v_y \frac{\partial s}{\partial y} - v_z \frac{\partial s}{\partial z}. \quad (2)$$

From continuity considerations, the expression in parentheses must be zero. However, since *Daphnia* tend to maintain their depth, their vertical velocity must be zero. This gives the whole expression a non-zero value which represents a departure from the equation of continuity. This is the key to the whole problem.

Let $v_z = 0$ to describe no motion by the *Daphnia*, and $v_y = 0$ by assuming the x direction to be that of the current. Simplifying, we obtain:

$$\frac{\partial s}{\partial t} = \text{Diffusion} - s \frac{\partial v_x}{\partial x} - v_x \frac{\partial s}{\partial x}. \quad (3)$$

The middle term on the right is the horizontal velocity divergence, and the last term is the horizontal transport or the advection of the plankton.

This equation says that the local change in concentration is due to the combined effects of diffusion, advection, and horizontal divergence. Diffusion acts only in the direction of decreasing concentration. Therefore it always tends to destroy variation and produce uniformity. Advection implies that variations already present will be transported past a given location according to the direction and magnitude of the currents. It cannot produce the variations. Horizontal divergence is the process that produces variation. With water alone this necessitates vertical currents, but with *Daphnia* we have already assumed that no

TABLE III.—NUMERICAL EXAMPLES

Sta.	Dates April	S Daphnia/ m^3	V cm/day $\times 10^5$	$\partial s / \partial x$ Daphnia/cm $\times 10^{-2}$	Div. 1/day	Advective term Daphnia/ m^3 /day	Divergence term Daphnia/ m^3 /day	Sum Adv. & Div. Daphnia/ m^3 /day	Observed Change Daphnia/ m^3 /day
9	22-23	9	1.5	-39.	0	+59,000	0	+59,000	+15,000
9	23-24	15,000	1.7	+23.	0	-20,000	0	-20,000	-14,300
37	22-23	48	2.4	-0.083	0	+200	0	+200	+201
37	23-24	249	1.6	0.0	-4.3	0	+1,070	+1,070	+1,640
35*	23-24	312	1.6	-0.86	+4.3	+1,400	-1,300	+100*	-228
24	22-23	11	0.52	-0.22†	+4.3	+110	-47	+63	+1,460

*Difference of two large numbers. An error of 300 in prediction represents a 20% error in either calculated term which is not in excess of the error to be expected.

† Gradient probably greater, but data missing at edge of *D. pulex* mass off Picnic Point; zooplankton contributing to this change undoubtedly came from beyond region of survey.

vertical motion exists. Therefore convergence will tend to increase the *Daphnia* concentration while divergence will tend to decrease it. Since we can measure convergence, we should be able to measure the rate at which the animals are concentrated.

As a numerical example we shall take several sets of data from the charts. A certain amount of judgment in the choice of data is necessitated by the limited size of the experiment. For example, data from the mouth of the Bay could not be used because the gradients up-current were not known. Since the current velocity decreases at night, the average current and divergence values were arbitrarily reduced by one-half. Starting, then, with the plankton concentration and gradient for the first of a pair of days, Table III compares the expected change with that actually observed in the subsequent 24 hours.

The results in Table III show that advection is dominant at Station 9 in both cases and at Station 37 for April 22-23. Divergence is dominant of Station 37 for April 23-24. At Station 35 both processes are operating at similar rates but in opposite directions. The calculation for Station 24 is presented to show how extrapolation of the plankton gradient beyond the region of survey may lead to erroneous results. Thus one or the other or both of these processes may be important in the distribution of the zooplankton.

Acknowledgement. The authors would like to express their appreciation to Peter M. Kuhn and Charles R. Stearns for invaluable assistance on the project.

Conclusions:

1. Large horizontal variations of the zooplankton in Lake Mendota do exist.
2. Study of the zooplankton distribution reveals its close relation to the currents and especially to the simultaneous effects of divergence and the phototactic response of the animals.
3. The combined processes of mechanical concentration and transport of zooplankton must be kept in mind during any attempt to sample the zooplankton population of Lake Mendota and probably other lakes of similar size.
4. The phenomenon may be described by an equation which can be evaluated from actual field measurements of plankton concentration and current velocity distribution.

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FURTHER OBSERVATIONS ON THE BREEDING AND MIGRATION OF THE BERMUDA SPINY LOBSTER, *PANULIRUS ARGUS*¹

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ABSTRACT

Some results of investigations of breeding, distribution, and migration of *Panulirus argus* in Bermuda during 1951 and 1952 are given. A graphic schedule of breeding events for females includes the times of appearance of the first and second spermatophores and the first and second eggs. Certain aspects of mating and the shedding of pleopodal setae by females are discussed. Lobsters larger than 145 mm carapace length are found most frequently in the lagoon and are in notably small proportions outside the reefs. This distribution is particularly noticeable during the breeding season when most of the smaller mature lobsters migrate to the periphery of the reefs. Data indicate a correlation of color of lobster and environment.

INTRODUCTION

While the observations presented here are based in part upon investigations begun in 1949 by E. P. Creaser, they are mainly a continuation of work published in a previous paper dealing with breeding and migration of the Bermuda spiny lobster (Sutcliffe, 1952). The work was supported throughout by a grant from the Bermuda Government and has constituted a staff project of the Bermuda Biological Station.

The author gratefully acknowledges the assistance of Mr. Jack O'Connor, Mr. Michael Scott, and the rest of the staff of the Bermuda Biological Station. Thanks are also due Mr. Edric Spurling, who furnished much valuable information.

METHODS

The lobsters for this investigation were obtained from traps confined mostly to a two-mile wide section across the Bermuda plateau, including North Rock to the north, Ferry Reach, Castle Harbor, and Nonsuch Island on the south shore (Fig. 1). During the summer of 1952 correlative material was obtained from traps located at various other places (see Fig. 1). All measurements are in terms of carapace length in millimeters.

¹ Contribution No. 196 from the Bermuda Biological Station.



Figure 1. Bermuda and reefs showing locations of traps: enclosed area near Nonsuch Island represents seven or more traps maintained the year round; O, isolated year-round traps; X, maintained summer 1952; □, maintained intermittently; A, North Rock; B, lagoon; C, North Shore; D, Ferry Reach; E, Castle Harbor; F, Nonsuch Island; G, South Shore; H, Harrington Sound. The dotted lines represent the three-fathom contour.

RESULTS AND DISCUSSION

Breeding. Females are seldom found in breeding condition at carapace lengths of less than 90 mm; sexual maturity is attained at 90 to 95 mm (Sutcliffe, 1952). Percentages of females 95 mm or larger in the various phases of breeding are shown in Fig. 2. It may be seen that although all of the females laid their first brood, they were not all carrying their first eggs at any one time. The mode of the second laying is of lesser magnitude, possibly because all of the females did not lay eggs a second time. Also, it is possible that females carried the second set of eggs for a shorter length of time because of rising temperatures (maximum in August), thus making the percentage of females carrying the second eggs smaller at any one date. The percentage of females showing signs (see Sutcliffe, 1952) of having carried

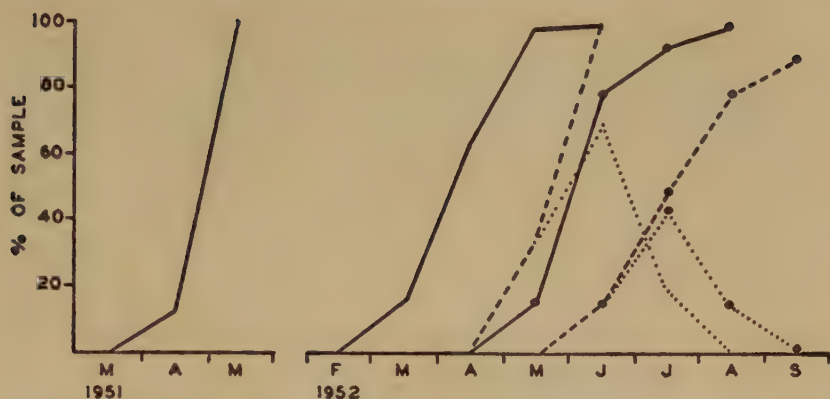


Figure 2. Percentages of females 95 mm and larger (539 specimens) in various phases of breeding: — with first spermatophore; —○— with second spermatophore; actually carrying first eggs; actually carrying second eggs; — — — showing signs of having carried first eggs; —○— showing signs of having carried second eggs.

eggs in September may not be indicative of a true percentage value of the total fecund population, for by this time some of the females had undergone ecdysis following the breeding season and thereby obliterated the criteria for determining the previous breeding history.

Repetitive egg laying has been noted for *P. argus* by Creaser (1950) and Sutcliffe (1952) and for *P. japonicus* by Ino (1950). In the last case only four of the 61 lobsters retained in the laboratory laid eggs for the second time. However, the attenuation and shape of the curve given by Ino, expressing percentages of egg-bearing females during the breeding season, suggest that a considerable number of Japanese lobsters may lay a second time. Smith (1951) has given a graph of percentages of egg-bearing females for *P. argus* in the Bahamas, as has Bradstock (1950) for *Jasus lalandii* in New Zealand. In Smith's and Bradstock's material the curves are essentially bimodal, thus indicating a second laying. In both cases the second peaks are smaller than the first, hence these observations tend to agree with those in Bermuda.

If the appearance of the first spermatophore in 1951 is compared with the first in 1952 (Fig. 2), it may be seen that active mating for the majority of lobsters took place about a month earlier in 1952. A possible explanation for this may be seen in Fig. 3, which shows that surface temperatures as recorded in Ferry Reach during March and April were higher earlier in 1952 than in 1951.

Ten matings involving the deposition of the first spermatophore were obtained in the laboratory, although the matings were not actually observed. All laboratory matings took place when both

male and female were in a completely hard-shelled condition. Furthermore, all females brought in from the field with freshly deposited spermatophores were hard-shelled. It has also been noted (Sutcliffe, 1952) that the second mating is not preceded by moulting. But the hard-shelled condition of the female may not be invariable, for Craw-

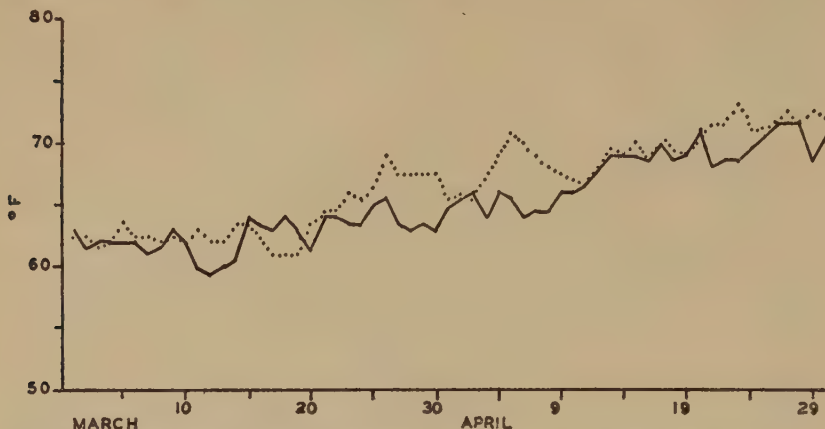


Figure 3. Daily surface water temperatures in Ferry Reach in March and April: —, 1951; ·····, 1952.

ford and De Smidt (1922) reported the case of a female carrying a spermatophore while the shell was "quite soft," which indicates that mating took place soon after moulting. Sheard (1949) says of *P. longipes*, "To be successful mating must occur immediately after the moult of the female while the shell is still soft." The mating of *Jasus lalandii* takes place when the female is in a soft-shelled condition (von Bonde, 1936). Thus, although the soft-shelled condition of the female during mating is known for two related species, the hard-shelled condition of females during mating seems to prevail with *P. argus*.

It is possible that the stimulus for the extrusion of the eggs is not a function of mating with *P. argus*, for laying occurred from a few days to a month after mating in the laboratory. Two unmated females retained in the laboratory laid unfertilized eggs. These remained attached only a few days. Unmated females of *Palaeomonetes* are known to lay eggs as well (Burkenroad, 1947). Field results indicate that egg-laying by lobsters occurred a little over a month following mating (Fig. 2).

Starting in November 1951, females were examined as to the condition of the endopodal setae of the pleopods which carry the eggs. The hatching of the second eggs in August was followed by an ecdysis

TABLE I. MONTHLY CATCHES OF FEMALE LOBSTERS (95 mm or more) AND
CONDITION OF PLEOPODAL SETAE

Date	Premoult	Postmoult		Percentage of postmoult with short setae
	Spermatophore remnants and long setae	No spermatophore remnants Long setae	Short setae	
1951				
Nov.	5	12	6	33
Dec.	0	21	1	5
1952				
Jan.	0	51	4	7
Feb.	0	76	0	0
July	84	0	0	0
Aug.	39	1	0	0
Sept.	36	2	2	50
Oct.	9	7	1	13
Nov.	5	10	3	23
Dec.	0	37	4	10
1953				
Jan.	0	50	0	0

starting in September, as indicated by the disappearance of the remnants of the used spermatophores (see Table I). In decided contrast to the long setae of breeding females, a number of adult females subsequently appeared with the pleopodal setae reduced to short bristles, a reduction on the average from 13 to 1 mm in length. This condition is not found to be restricted to any particular size of adult animal. The shedding of the female abdominal breeding plumage, not unusual in decapods, has been reported for *Panulirus japonicus* by Nakamura (1940); but apparently this is not the case with *Jasus lalandii*, for Bradstock (1950) has pointed out that reduced setae are found only in the immature of this species. Of five females of *P. argus* which were kept in the laboratory and which underwent the first ecdysis after hatching of eggs, one retained the long setae essentially unchanged except for somewhat lighter color. The other four moulted to the short-seta condition. The three females which had long setae in August and September 1952 (Table I) could have undergone only one moult after egg hatching because of the short lapse of time involved; therefore they must have retained the setae. Thus, there would seem to be some variation with respect to the shedding of pleopodal setae among the females of *P. argus*. It is not known whether the cause is genetic or environmental.

Note also in Table I the progressive decline in the relative numbers of females with short setae in both 1951 and 1952. No females 95 mm or longer with short setae were observed from January 1952 until September 1952, which indicates that the females with reduced pleopodal setae (if not the entire adult female population) undergo a subsequent moult, evidently in the late fall or winter, which restores the long setae.

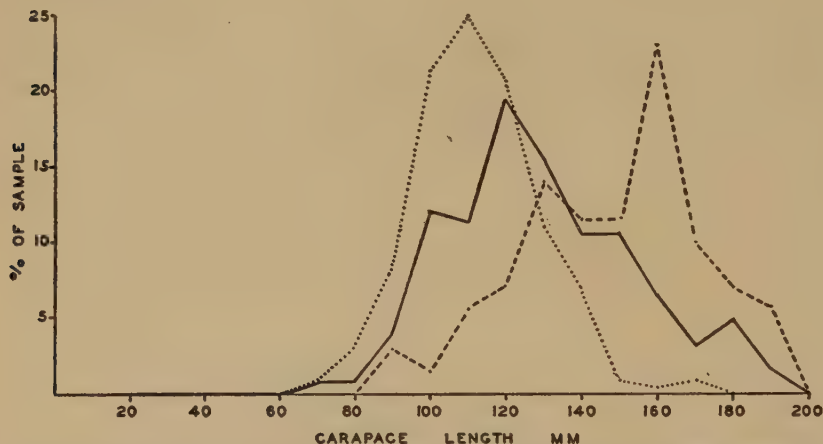


Figure 4. Comparison of length-frequencies: — lagoon population, September through April, 1951, 1952 (124 specimens); ---- lagoon population, May through August 15, 1951, 1952 (70 specimens); south shore population, November through February, 1951, 1952 (259 specimens).

Distribution and Migration. Sutcliffe (1952) has shown that certain sizes of the Bermuda spiny lobster become assorted at different depths or localities. The smallest immature lobsters are found in the shallowest protected inshore waters while the mature populations are more widely scattered. It is evident that there is further sorting with respect to lobsters of the largest sizes. Fig. 4 represents length-frequencies of animals sampled in two localities, the south shore and the lagoon. The dotted line shows the size composition of a representative sample of the population taken on the south shore in the Non-such area from November through February 1951. This is a fairly typical picture of the lobsters in waters less than 20 fathoms deep at the edges of the reefs, for samples taken at various times from the edges of the reefs of the east, northeast, northwest, and southwest were essentially similar. The south shore population varies slightly throughout the year with respect to the groups of greatest frequency,

and if the mode shifts at all, it is only between 115 and 120 mm in carapace length.²

The lagoon population contains considerably more lobsters of a larger size than does the population of the south shore (Fig. 4). Lobsters larger than 145 mm constituted about 26% of the fall-winter lagoon sample but only 3% of the south shore population; this discrepancy was even greater in summer. Although the south shore is moderately fished, this difference is not necessarily the result of fishing pressure, for a sample of 136 lobsters taken commercially from the reef edge to the northeast where there is relatively little lobster fishing showed that only 8% was 145 mm or larger. Furthermore, while the more central portions of the lagoon have long been known as a source of very large lobsters, none of the fishermen interviewed can remember having caught high percentages of large specimens on the outer reefs or beyond. Identical trapping methods are used in both places. Whether this concentration of large lobsters in the lagoon is a result of selective action on the part of the lobsters or is a matter of differential survival is not known. It is possible that the frequently heavy wave action at the reef edges could have deleterious effects on large individuals.

Further evidence of the peripheral breeding migration already discussed (Sutcliffe, 1952) may be seen in Fig. 4. If the sample taken in the lagoon from May to mid-August is compared with that taken there from September through April, a decided population shift is noted. Many of the lobsters smaller than 130 mm are lacking in the lagoon in summer; presumably they migrated to the reef edges. The remaining ones in the lagoon are mostly large males which do not migrate (82% in summer, 53% in fall-winter). Only an occasional female with eggs was encountered in the lagoon in summer, most of them having migrated to the reef edges and beyond. Correlative information from lobster collections obtained from a series of traps across the western end of the plateau (see Fig. 1) in the summer of 1952 confirmed this distribution. Egg-bearing females and males of a similar size were taken at the reef edges and down to 20 fathoms, while the lagoon was occupied mostly by large males and a thin scattering of immature specimens of both sexes. Very large males (190–200 mm) may be seen also in inshore situations such as Harrington Sound, Castle Harbor, and Ferry Reach.

The size composition of populations inhabiting water much deeper than 20 fathoms on the shelf of the Bermuda plateau is as yet unknown because of the practical difficulties of maintaining traps at such depths.

² This point will be discussed in a forthcoming paper entitled "Observation on the growth rate of the immature Spiny Lobster, *Panulirus argus*."

A few catches have been made at 50 fathoms, but the records are too scanty to warrant presentation at this time. From information given by Creaser and Travis (1950), it is apparent that lobsters can survive depths of at least 250 fathoms. According to Bradstock (personal communication), fishermen report large males and no females of *Jasus lalandii* in depths of 10–60 fathoms off New Zealand.

TABLE II. PERCENTAGES OF LIGHT AND DARK LOBSTERS FROM FIVE LOCALITIES IN BERMUDA (see Fig. 1)

Locality	% Dark	% Light	No. Specimens
South Shore	53	7	327
Ferry Reach and Castle Harbor	1	80	94
North Shore	5	42	77
Lagoon	11	25	168
North Rock	53	10	59

Certain practical aspects of this distribution of large and small lobsters come to mind. Inasmuch as there are indications that lobsters mate with others of a similar size, it would seem that the large males found in the lagoon contribute little with respect to breeding (females much larger than 140 mm are uncommon). The closed season on Bermuda lobsters (April 15–September 1) might be modified to trapping such males in the lagoon. Populations cannot be described as “overfished” purely on the basis of size composition without a careful search for possible distribution patterns such as those found in Bermuda, since the selection of certain areas at given seasons may furnish samples composed of lobsters of almost any size.

Both color and size seem to follow a marked distribution. Lobsters were divided into three arbitrary categories with respect to color—light, intermediate, and dark. The percentages of the extremes of variation are given in Table II for representative samples from five localities.

In general the coloration varies from very light (almost yellow) to nearly black and is characteristic of a given type of locality. This agrees with the findings of Crawford and De Smidt (1922) and Smith (1948) for *P. argus* and with those of von Bonde and Marchand (1935) for *Jasus lalandii*. Lobsters from the outside edges of the reef are characterized most frequently by an extremely dark hue while lobsters from inshore areas or inside the reefs assume lighter shades. As has been noted by Crawford and De Smidt (1922), it is definite that this is not a function of sex or size with *P. argus*, for the range of color variation has been observed in appropriate localities for all sizes of

both sexes. A similar conclusion was drawn for *P. interruptus* by Allen (1916). Sheard (1949) considers the extremely light-colored individuals of *P. longipes*, occurring most frequently in sandy areas adjacent to the reefs, to be "recently moulted virgin adults."

One might expect a seasonal change in percentages of dark and light animals in the south shore catches which would correspond to the migratory pattern. That is, during summer one would expect to find a greater number of light-colored lobsters in this area, but this does not seem to be the case. Although the total number of lobsters

TABLE III. NUMBERS OF LOBSTERS MOULTING IN THE LABORATORY, SHOWING FIELD COLORATION OR COLOR ASSUMED UNDER LABORATORY CONDITIONS
(D. TRAVIS, PERSONAL COMMUNICATION)

<i>Number of moults in laboratory</i>	<i>Field coloration retained</i>	<i>Laboratory coloration attained</i>
0	15	1
1	3	5
2	5	14
3	1	26
4	0	5

rises considerably as shown by increased catch per unit-of-effort, the percentage of light-colored individuals remains much the same. As has been suggested (Sutcliffe, 1952), it is possible that the outward summer migration from the lagoon may be opposed by an inward migration from the deep water of the shelf, thus canceling out changes in color percentages.

When a lobster is kept in the laboratory there is no readily apparent change of color until after the first moult. Even though lobsters of contrasting color are used, the original hue is invariably retained until after one or more laboratory moults. The coloration of lobsters after ecdysis in the laboratory tended to a light bluish-gray or lavender with considerable individual variation. Table III shows noticeable color changes in animals maintained in indoor tanks. It may be seen that with an increasing number of laboratory moults there is an increasing tendency toward the bluish or lavender cast. This suggests that the previously mentioned variations in field color would be a result of the animals' existence for a certain length of time under different conditions. Of lobsters taken in the field, the nearest approach to the laboratory type of coloration was found on those that inhabit caves.

SUMMARY

1. A graphic schedule of breeding events for females of *Panulirus argus* in Bermuda for the summer of 1952 includes the times of appearance of the first and second spermatophores and of the first and second eggs as well as the approximate lengths of time that the two sets of eggs are carried. Repetitive egg laying is discussed with respect to this and some other species.

2. Active mating, as indicated by the appearance of the first spermatophores, began earlier in 1952 (March) than in 1951 (April). It is suggested that an earlier rise in temperature in 1952 may have been a contributing factor.

3. Available evidence indicates that *P. argus* mates while both sexes are in a hard-shelled condition. In two related species the female is soft-shelled during mating.

4. It is possible that mating is not a stimulus for the laying of the first set of eggs, since females in the laboratory laid eggs from a few days to a month after mating; two unmated females laid eggs.

5. Part of the adult female population sheds the pleopodal setae with the first moult following breeding. These setae are restored on a subsequent moult. The percentage of females that shed the setae is not known with certainty.

6. In addition to the localization of immature lobsters there is a sorting of large lobsters, particularly males. Thus far the latter individuals have been found most frequently in the lagoon. Adequate information is lacking for waters deeper than 20 fathoms outside the reefs.

7. The size distribution of large lobsters is most noticeable in the breeding season when the great majority of mature females and smaller mature males migrate to the periphery of the reefs. Certain practical aspects of this distribution are discussed.

8. Data show that the majority of lobsters in a given area tend to assume a characteristic color which may vary from nearly black to almost yellow. Darkest lobsters are found at the reef edges; lightest individuals are found inshore and in the lagoon. These color variations are not a function of size or sex and are probably a result of their existence for a certain length of time in a given type of locality.

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EXAMPLES OF THE POSSIBLE ROLE OF INERTIA AND STRATIFICATION IN THE DYNAMICS OF THE GULF STREAM SYSTEM¹

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ABSTRACT

An hypothesis is offered to explain certain major features of the Florida Current: (1) the large axial gradient of vorticity, (2) the fact that seasonal fluctuations in the Miami-Cat Key tide gauge difference are twice the amplitude of those in the Key West-Havana tide gauge difference, and (3) the fact that the Havana-Cat Key difference is at a maximum during the period of minimum flow—the opposite of what might ordinarily be expected. An elementary perturbation theory of meanders in a wide stratified current is presented and its possible application to Gulf Stream meanders is discussed.

1. *Introduction.* Recent successful oceanographic studies of the steady-state wind-driven ocean circulation (Munk, 1950; Hidaka, 1949) do not require inclusion of the effects of density stratification or of inertia terms. Transient or periodic phenomena in general involve both inertia and stratification explicitly, and it seems to this author that results obtained from theoretical consideration of homogeneous models may omit important features. For example, Ichiye (1951) has obtained an interesting solution for the wind-driven ocean circulation due to a periodic wind-stress acting on a homogeneous ocean. In a stratified ocean, however, the mass movements which must accompany changes in the circulation are many hundredfold those occurring in a homogeneous ocean, and changes in potential energy are correspondingly greater. This raises the question as to whether or not the time-constants which characterize the response of a stratified ocean to a periodic wind-stress will be the same as those obtained by Ichiye's solution. This paper does not attempt to answer this difficult question. Instead, it treats two problems, the mass distribution of the Florida Current and the stability and size of Gulf Stream meanders, in which stratification and inertia play essential roles.

2. *Florida Current Tide and Current Data.* Numerous studies of tide gauge data have been made (Montgomery, 1938, 1941; Iselin, 1940; Hela, 1952) to obtain information about seasonal fluctuations

¹ Contribution No. 645 from the Woods Hole Oceanographic Institution.

in the cross-stream slope of the sea surface, and, by the geostrophic equation, to compute seasonal fluctuations of the mean surface velocity of the Florida Current. In addition to the tide gauge data already published for Key West, Miami, and Cat Key, tide gauge data for Havana are now available for the first time. These data are obtained from a gauge installed by the U. S. Coast and Geodetic Survey in 1946. Table I shows the monthly means of sea level (in feet)

TABLE I. MONTHLY MEANS OF SEA LEVEL (FEET), EACH REFERRED TO SEPARATE LOCAL DATUM

<i>Month</i>	<i>Cat Key</i> 1938- early 1941	<i>Key West</i> 1930-1948	<i>Havana</i> 1947-1951	<i>Miami Beach</i> 1935-1944
Jan.	3.75	4.88	4.82	3.34
Feb.	3.77	4.83	4.80	3.34
Mar.	3.82	4.82	4.92	3.22
Apr.	3.90	4.93	4.95	3.34
May	3.94	5.01	5.10	3.48
Jun.	3.98	5.03	5.09	3.41
Jul.	4.07	5.03	5.06	3.33
Aug.	4.18	5.17	5.26	3.46
Sep.	4.29	5.37	5.37	3.79
Oct.	4.18	5.53	5.47	4.07
Nov.	3.94	5.33	5.06	3.84
Dec.	3.84	5.06	4.94	3.74

measured at these stations, averaged over different sets of years, uncorrected for atmospheric pressure, and each referred to a different datum. A leveling survey has been made between Key West and Miami (Montgomery, 1941), but obviously it is impossible to connect Havana or Cat Key to the same datum by ordinary means. Therefore we cannot obtain true differences in sea level across the Straits, but we can obtain fluctuations in the differences of sea level at two stations, as shown in Fig. 1. At all four stations there is a maximum sea level in September-October which is apparently caused by the summer heating of the water. This average rise does not appear in the differences.

It is interesting to note that the fluctuation in the Miami-Cat Key differences is about twice that of the Key West-Havana differences. The maximum cross-stream slopes occur during July when the flow is strongest (Fuglister, 1951), at which time the maximum downstream slope from Key West to Miami also occurs. These relations of slopes to surface velocity are quite what might be expected from the most elementary considerations of Bernoulli's equation and the geostrophic

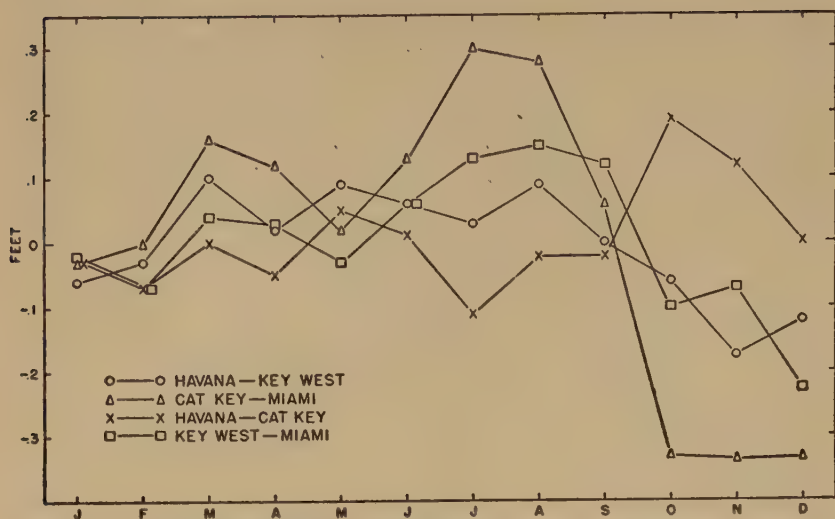


Figure 1. Monthly mean tide gauge differences for various pairs of stations, adjusted so that the annual mean of the differences vanishes.

equation. But at first sight it is rather startling that the fluctuations of the differences at Miami-Cat Key are larger than those at Key West-Havana and that the downstream slope between Havana and Cat Key is smaller in July rather than larger, hence an explanation is required.

Another noteworthy feature of the Florida Current is the extensive region of anticyclonic vorticity in the section off Miami. So far as direct velocity measurements from an anchored vessel are concerned, the data are scanty. The only observations at different depths are those of Pillsbury (1890), and these show a rapid decrease of velocity with depth. The axis of maximum surface velocity is not in the center but is displaced toward Miami; and this feature has been verified from many crossings of the Current off Miami by Murray (1952). Fig. 3 shows measurements with towed electrodes during one of these crossings, but it should be emphasized that towed electrodes are apt to give particularly misleading readings of velocity in the Florida Straits. Nevertheless, the general fact is that a wide zone of anticyclonic vorticity (of approximately $-[0.5 \pm 0.1]f$, where f is the local Coriolis parameter) seems to be established and also requires explanation. It is impossible, of course, for the variation of the Coriolis parameter with latitude to cause such shear over so short a distance as the length of the Florida Straits.

The channel at Miami is only about half as deep and half as wide as that at Key West, as shown in Fig. 2. The change in depth can

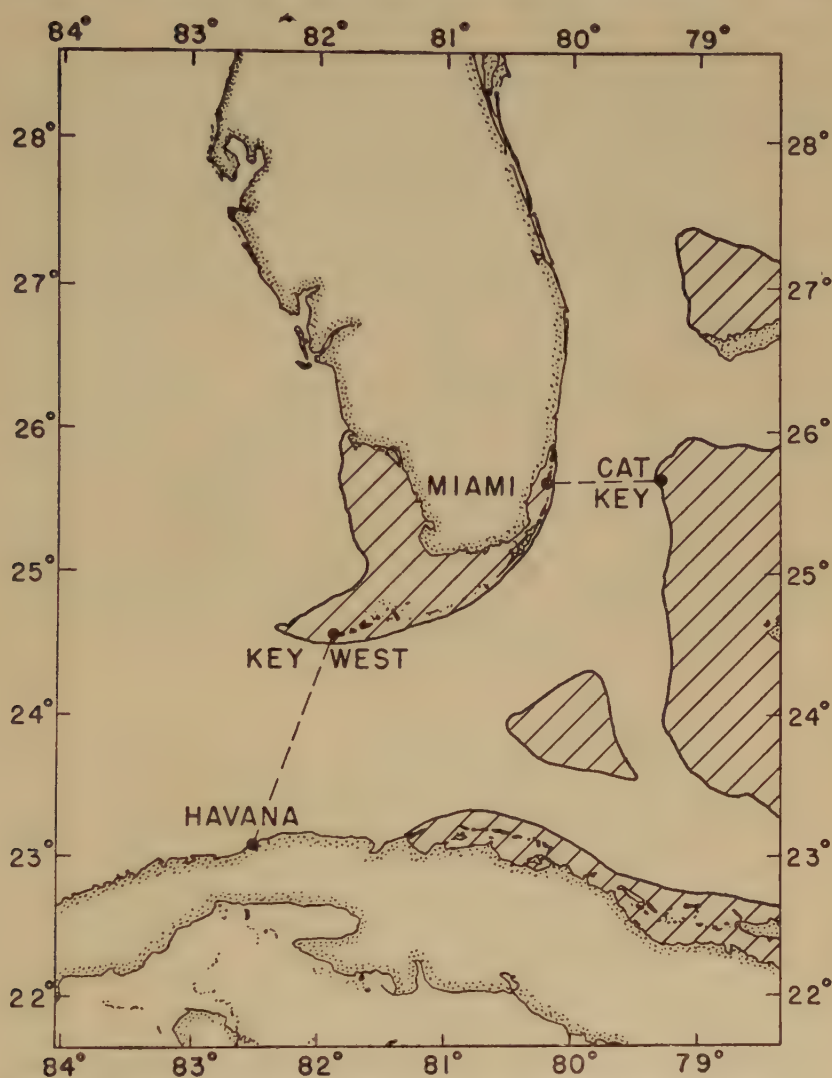


Figure 2. Chart of the Florida Straits showing the positions of the tide gauges.

have no important influence on the flow because the bottom water does not have an appreciable velocity at either section. On the other hand, the narrowing of the channel at Miami is important hydrographically because the water, in order to pass through it, is accelerated, and this requires a small drop in the level of the free surface from Key

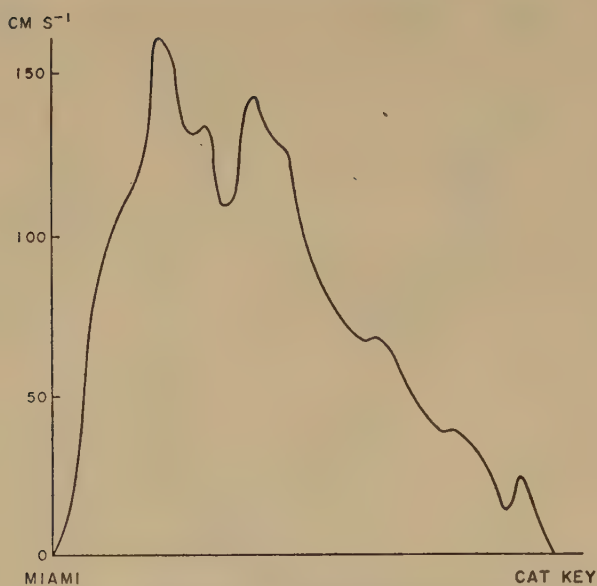


Figure 3. One of Murray's cross-stream surface velocity profiles made across the Florida Current off Miami.

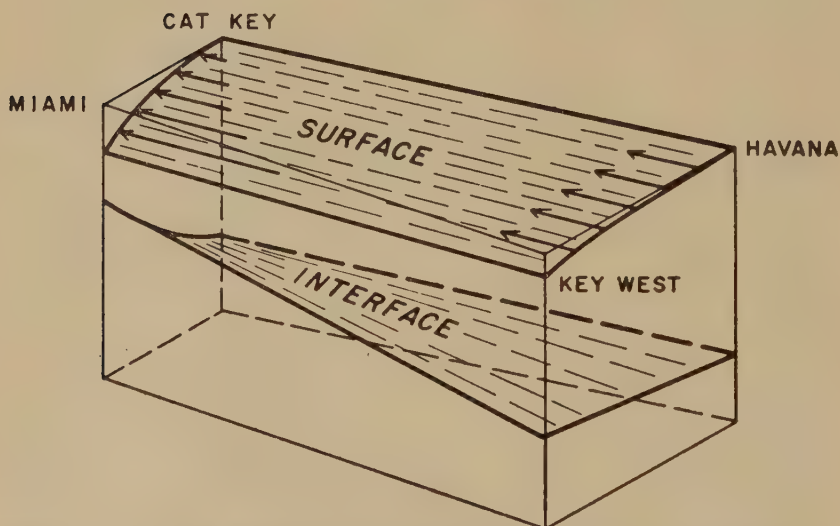


Figure 4. Schematic diagram showing configuration of the free surface (exaggerated scale) and of the interface in the hypothetical model of the Florida Current.

West to Miami. Since the lower layers are at rest (except for tides), the isopycnic surfaces must slope upward from Key West toward Miami to counteract the axial pressure gradient in the upper accelerating layers. Because this slope must be some 500 times the drop of the free surface, it produces a marked decrease in the thickness of the surface layers as Miami is approached. By virtue of the principle of conservation of absolute vorticity, this vertical shrinking produces an anticyclonic shear and magnifies the transverse geostrophic slope of the free surface. A crude quantitative analysis based on a two-layer model is presented in the following section. Fig. 4 illustrates the average hydrographic structure of the Florida Current envisaged in this hypothesis.

3. *Application of the Vorticity Theorem to the Florida Current.* Consider a layer of water of density ρ_1 , depth D , overlying a deep resting layer of density ρ_2 . The upper layer has a velocity U at the Key West-Havana section ($x = 0$) and its vorticity is taken as zero. Further downstream ($x = \Delta x$), at the narrower Miami-Cat Key section, the stream has accelerated by a drop in the free surface Δh . Because the lower layer is at rest, the interface must slope upwards to offset the effect of the free surface. If the axial pressure gradient vanishes in the lower layer then the following relation must hold:

$$\frac{\rho_2 - \rho_1}{\rho_2} \frac{\partial D}{\partial x} = \frac{\partial h}{\partial x}.$$

The vorticity equation in this simple case may be written as follows, where ζ is the vorticity of the upper layer:

$$U \frac{\partial}{\partial x} \left(\frac{\zeta + f}{D} \right) = 0,$$

where a steady state of motion is presumed. Since the vorticity vanishes at Key West, that at Miami is given approximately by

$$\Delta \zeta = f \frac{\Delta h}{D} \frac{\rho_2}{\rho_2 - \rho_1}.$$

The actual acceleration observed at Miami corresponds to a value of Δh of about -20 cm (this is somewhat in excess of the -4.9 cm obtained by leveling between Key West and Miami, according to Montgomery, 1941). The density difference of the two layers is approximately $(\rho_2 - \rho_1)/\rho_2 \cong 2 \times 10^{-3}$. The initial depth D of the current is roughly 250 m, which yields a value of the vorticity increase between Key West and Miami of $\Delta \zeta \cong -0.4f$, which corresponds

within the limit of observational error to the observed value given above.

If the high anticyclonic vorticity at Miami is actually due to the vertical shrinking of the upper layers, then it should be possible to test this hypothesis by careful hydrographic observations on the two sections to try to detect the average rise of about 100 m in the isopycnic surface at 100–300 m depth. It will be difficult and tedious to measure this hypothetical rise because it may be partly masked by the large cross-stream slope of the isopycnic surfaces and by variations in depth due to tides. Present data are insufficient to attempt a satisfactory test.

4. *Gulf Stream Meanders.* The Gulf Stream meanders observed on the Multiple Ship Survey of June 1950 (Fuglister and Worthington, 1951) have inspired several theoretical studies. It has been suggested that they are analogous to the waves in the atmospheric jet stream, but both their small scale (100–400 km) and small velocities of propagation suggest that the variation of the Coriolis parameter with latitude is not a dominant factor in their dynamics. Haurwitz and Panofsky (1950) have constructed several models of currents in a homogeneous ocean with cross-stream velocity profiles similar to those observed in the true Gulf Stream and have carried out an intricate perturbation analysis to show the existence of unstable waves with reasonable velocities of propagation. These waves are a result of the shearing instability of the Stream.

It seemed to the writer that, if stratification were taken into account, certain types of meanders might exist in which horizontal divergence was dynamically important. In order to illustrate such a system, meanders in a wide current were studied. To simplify the analysis, the realistic cross-stream velocity profiles of Haurwitz and Panofsky were abandoned. The density stratification of the real ocean is approximated by a two-layer system such as that used in Section 3.

5. *A Simple Meander Theory for a Wide Current in a Stratified Ocean.* Let us suppose that the lower layer is sufficiently deep so that the horizontal pressure gradients vanish in it at all times. In the undisturbed state a steady current U flows in the x -direction in the upper layer. Associated with this current is a cross-stream pressure gradient of the following form:

$$fU = -g \frac{\partial h}{\partial y} = -g \frac{\partial D}{\partial y} \frac{\Delta \rho}{\rho}.$$

We now suppose that small perturbations, u , v , the velocity components, and h , the elevation of the free surface, occur, and that these

quantities are independent of y , the cross-stream co-ordinate. The perturbation equations may be written in the form:

$$\left(\frac{\partial}{\partial t} + U \frac{\partial}{\partial x}\right) u - fv = -g \frac{\partial h}{\partial x}, \quad (1)$$

$$\left(\frac{\partial}{\partial t} + U \frac{\partial}{\partial x}\right) v + fu = 0, \quad (2)$$

$$\left(\frac{\partial}{\partial t} + U \frac{\partial}{\partial x}\right) \left(\frac{\rho}{\Delta\rho} + 1\right) h + D \frac{\partial u}{\partial x} + v \frac{\partial D}{\partial y} = 0. \quad (3)$$

If the perturbations are all in the form $e^{i(kx - \sigma t)}$, we obtain the following frequency equation, taking $f = \text{constant}$:

$$k^2 U^2 (1 - p)^3 - \left[f^2 + gk^2 \frac{\Delta\rho}{\rho} D \right] (1 - p) + f^2 = 0,$$

where $p = \frac{c}{U} = \frac{\sigma}{kU} = p' + ip''$, the real part (p') of which is the ratio of the velocity of propagation of the wave to the velocity of the current, and the imaginary part (p'') of which gives the instability of the wave motion. For the particular range of parameters involved, no one of these terms is small compared to the others. It is convenient to rewrite this equation in the form:

$$y^3 + 2 = \mathbb{I}y,$$

where $\mathbb{I} = 2 \left(\frac{f^2}{2k^2 U^2} \right)^{\frac{1}{2}} \left(\frac{f^2 + gk^2 \frac{\Delta\rho}{\rho} D}{f^2} \right)$ and $y = \left(\frac{f^2}{2k^2 U^2} \right)^{-\frac{1}{2}} (1 - p)$.

The roots of this equation are all real provided $\mathbb{I} \geq 3$, in which case there are three types of stable waves present. If $\mathbb{I} < 3$, there is a region of unstable waves. These are of most interest to us because they are the only ones that are likely to grow large enough to be noticed on a ship survey. Examination of the coefficients of the frequency equation reveals that for $U^2 < g \frac{\Delta\rho}{\rho} D$, all waves are

stable. At $U^2 = g \frac{\Delta\rho}{\rho} D$, a single wave number given by $k = f/(\sqrt{2} U)$ becomes "just unstable," whereas all other wave numbers are stable. For slightly larger values of U^2 there is a narrow range of wave numbers about $k = f/(\sqrt{2} U)$ in which waves are unstable. In the critical case of marginal stability the "just unstable" wave is stationary.

One objection to the application of this model to the meanders observed in the Gulf Stream is that the real Stream is not very wide. A more sophisticated theory would include lateral boundaries to the Stream and would provide for resting layers of water on each flank beyond the boundaries. Also a perturbation theory such as this applies only to waves of infinitesimal amplitude, whereas meanders often grow to large amplitude. Therefore it is important to regard this treatment of meanders as merely indicative of the possible role of divergence terms in the meandering of a stratified current. Their physical reality must be tested by actual observation of the depth of the current in the crests and troughs of meanders.

6. *Application to the Actual Gulf Stream.* Rossby (1951) has shown that velocity of the Gulf Stream does in fact approach the critical

value $\sqrt{g \frac{\Delta\rho}{\rho} D}$. In a steady state one might expect the Stream to

become progressively shallower downstream, gradually approaching the critical condition. Because of the paucity of hydrographic sections of the Stream in any one year or season it is necessary to construct a composite series of sections in order to determine whether or not there is a noticeable change in the depth of the Stream along its axis. A number of sections, all made in early June of several years, have been assembled and recomputed: (1) one at Hatteras at about 74° W; (2) two more on the Montauk Point to Bermuda line surveyed in Iselin's (1940) studies; (3) one at 58° W; and (4) two Ice Patrol sections along the 50° W meridian. The geostrophic transports at different depths were computed. In order to exhibit any changes in the depth of the Stream, the percentage of the total transport below certain selected depths was computed. The results are given in Table II; it is clear that there is no striking change in the depth of the Stream as indicated by these sections. The inference to be drawn from this is that the Stream is near to the critical velocity almost everywhere from Cape Hatteras to the tail of the Grand Banks and that unstable meanders of a single wavelength might be expected anywhere.

We may ask ourselves what the size of the meanders predicted by our two-layer meander theory might be expected to be. A surface layer 200 m thick moving at 200 cm sec⁻¹ and having a density difference ratio of $\Delta\rho/\rho = 2 \times 10^{-3}$ is critical. The wavelength of the "just unstable" perturbation corresponding to this choice of parameters is 180 km. All other wavelengths are stable and do not grow. It is remarkable that this wavelength corresponds closely to that of

the large stationary meander which was observed during growth and detachment into an eddy (Fuglister and Worthington, 1951).

During the process of growth this observed meander diverted momentum at right angles to the mean direction of the Stream; from mixing-length ideas we may calculate the order of magnitude of the local gross coefficient of lateral eddy viscosity due to this eddy: $A = U 2\pi/k$, where k is wavelength of the detaching meander. Sub-

TABLE II. PERCENTAGE OF TOTAL TRANSPORT BELOW SELECTED DEPTHS AT DIFFERENT HYDROGRAPHIC SECTIONS ALONG THE GULF STREAM
(AT. = ATLANTIS; IP. = ICE PATROL)

Depth (m)	74° W AT. 4570- 4565	68° W AT. 2871- 2867	68° W AT. 3053- 3054	58° W AT. 2620- 2616	50° W IP. 2715- 2719	50° W IP. 4175- 4184
0	100	100	100	100	100	100
50	94	92	92	92	91	92
100	88	85	84	84	82	84
200	74	71	69	69	65	69
300	61	58	55	56	50	56
400	49	46	43	44	37	45
600	30	38	23	26	19	28
900	12	13	7	9	6	12
1200	4	7	2	3	2	4
1600	1	1	0	1	0	1
2000	0	0	0	0	0	0

stituting numerical values above, we obtain $A = 3.6 \times 10^9 \text{ cm}^2 \text{ sec}^{-1}$, a value much in excess of that used by Munk (1950) in his wind-driven ocean circulation theory. If it is recalled that Munk assumed a uniform viscosity over the entire length of the Gulf Stream System and if it is assumed that there is usually but one detaching eddy at a time, then the discrepancy is not so glaring. The above value of A acts on only 90 km of the Stream, but if it is averaged over the entire length of 4,500 km, a value of $7 \times 10^7 \text{ cm}^2 \text{ sec}^{-1}$ is obtained which agrees rather well with Munk's value 5×10^7 . It is inferred, therefore, that the meanders alone produce sufficiently large scale lateral mixing processes for Munk's theory of the climatological mean Gulf Stream.

Since a thin filament of anomalously fresh water preserves its integrity all along the Gulf Stream proper (Ford, Longard, and Banks, 1952), it seems that the influence of mixing processes of a scale smaller than meanders must be negligible. The physical explanation of the process which determines the width and vertical structure of the instantaneous Gulf Stream is quite obscure.

In concluding, it is important to emphasize that the meander theory presented here is not complete or proven. It is merely suggestive of a type of wave-motion which may possibly dominate the dynamics of meanders. It is interesting to note that if the energy of meanders is absorbed from the potential energy of the cross-stream mass distribution instead of from the kinetic energy of the flow, the meanders are then a part of the thermohaline circulation of the ocean.

ACKNOWLEDGMENT

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CIRCULATION IN A MERIDIONAL PLANE IN THE CENTRAL EQUATORIAL PACIFIC

By

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ABSTRACT

Meridional sections of σ_t , salinity, inorganic phosphate, and dissolved oxygen, based on new data from the central equatorial Pacific, show evidences of upwelling near the equator. An Equatorial Front in the ocean surface layer is described. Sinking occurs along this front, which is found most often just north of the equator. Reasons are advanced for the existence of horizontal convergence and sinking in a region slightly to the north of the equator during southeast tradewinds when no front is present. Horizontal divergence and convergence apparent in a qualitative model of horizontal flow near the equator seem to be important in producing vertical motion. The circulation in a meridional plane in the surface layer is discussed, with strict adherence to the principles of isentropic analysis. The role played by the circulation in supporting a large population of zooplankton and fishes is discussed.

INTRODUCTION

Currently the U. S. Fish and Wildlife Service, through its Pacific Oceanic Fishery Investigations program (POFI), is investigating the tuna resources of the central equatorial Pacific Ocean (Sette, 1949). Since knowledge of the ocean circulation is basic to an understanding of such a study of productivity, the program includes an investigation of the physical and chemical environment. From January 1950 through August 1952, the HUGH M. SMITH occupied 365 hydrographic stations comprising a number of sections across the equatorial current system (see Fig. 1).

Measurements of the following were made at sea: temperature, using deep-sea reversing thermometers; inorganic phosphate, using the Automatic Servo-operated Photometer (Snodgrass, et al.); and oxygen by the Winkler titration. Water samples were taken to the Honolulu laboratory for chlorinity determination by the Knudsen method. Part of the large amount of hydrographic data collected has been examined in an attempt to determine the circulation in a meridional plane across the major equatorial currents.

Defant (1936) has described a model which he suggests illustrates the basic features of the meridional circulation of the tropical Atlantic, and Sverdrup, et al. (1942) and Sverdrup, et al. (1944) have stated

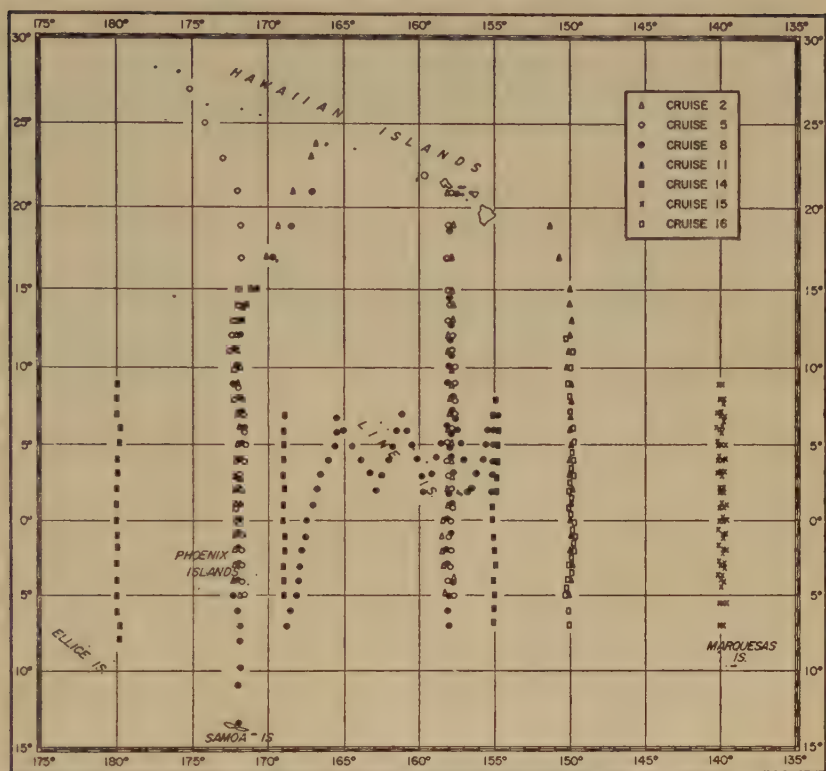


Figure 1. Positions of 365 hydrographic stations occupied by the M/V HUGH M. SMITH during seven cruises to equatorial waters. The cross sections of Fig. 2 are based on cruise 2 stations (Δ) along primarily 172° W Long. Those of Fig. 3 are based on cruise 5 stations ($\circ$) along 158° W Long.

that the same circulation exists in the Pacific. Montgomery (1938) has raised serious doubts that a circulation of the type they describe exists in the tropical Atlantic and Pacific. He has demonstrated the importance of isentropic analysis of flow in the ocean and its application to the meridional circulation. The qualitative discussion which follows is intended to adhere rigorously to isentropic principles.¹

Our data were examined first for evidence of vertical motion. The regions of upwelling and of sinking are revealed on cross sections like those shown in Figs. 2 and 3.

¹ In this paper the principles of isentropic analysis are applied to flow on surfaces of constant σ_t . For a discussion of the degree of inadequacy of σ_t surfaces to represent surfaces along which sea water flows, see Montgomery (1938: 11-14).

HORIZONTAL DIVERGENCE AND UPWELLING

The dense surface water that appears near the equator (Figs. 2 and 3) contrasts strikingly with adjacent surface water and suggests upwelling. Charts of sea surface temperature, such as those of Schott (1935) and Sverdrup, et al. (1942), show this feature as a band of cold water along the equator that decreases in prominence toward the west. This meridional contrast may be maintained in part by a strong west current at the equator, as drawn by Schott (1935), the water from the east being relatively dense. This does not seem to be the entire explanation, however, since the high concentration of inorganic phosphate in this dense water probably cannot be explained on the basis of horizontal flow from a source of nutrient-rich surface water at even the closest land to the east. At 50 miles per day it would take approximately 80 days for a parcel of water to reach the central Pacific from the Galapagos region, and during this time it is likely that the phytoplankton would deplete the inorganic phosphate were there not a continuing renewal from below.

Kinematically, this renewal clearly can take place along σ_t surfaces. The $\sigma_t = 23.60$ surface, which in Fig. 2 intersects the sea surface at two points near the equator, submerges both northward and southward into the thermocline. Meridional flow along this surface in either direction would bring water from the region of the thermocline to the sea surface near the equator. Thus, referring again to Fig. 2, flow of water which lies between the surfaces $\sigma_t = 23.60$ and $\sigma_t = 23.80$ may be likened to flow through a conduit that broadens vertically near the equator. Water within this layer which nears the equator from the south rises to the surface, its nutrients becoming available to plants in the euphotic zone. Further, some of this water may leave the euphotic zone, submerging as it continues northward within the "conduit." Vertical motion, then, can go on continuously with flow along σ_t surfaces and a stationary distribution of mass. Like most analogies this one should not be carried too far, however. Flow actually occurs through the "conduit walls," i. e., across surfaces of constant σ_t , as will be described later.

The same general features of density distribution that appear in Fig. 2 appear also in Fig. 3, although a pocket of relatively light water centered between 2° and 3° N complicates slightly the picture north of the equator.

There are several tongue-like features on the cross sections, particularly in the salinity distributions. Little information about flow can be inferred from these features, however, without information about the mixing processes which may be of major importance in maintaining

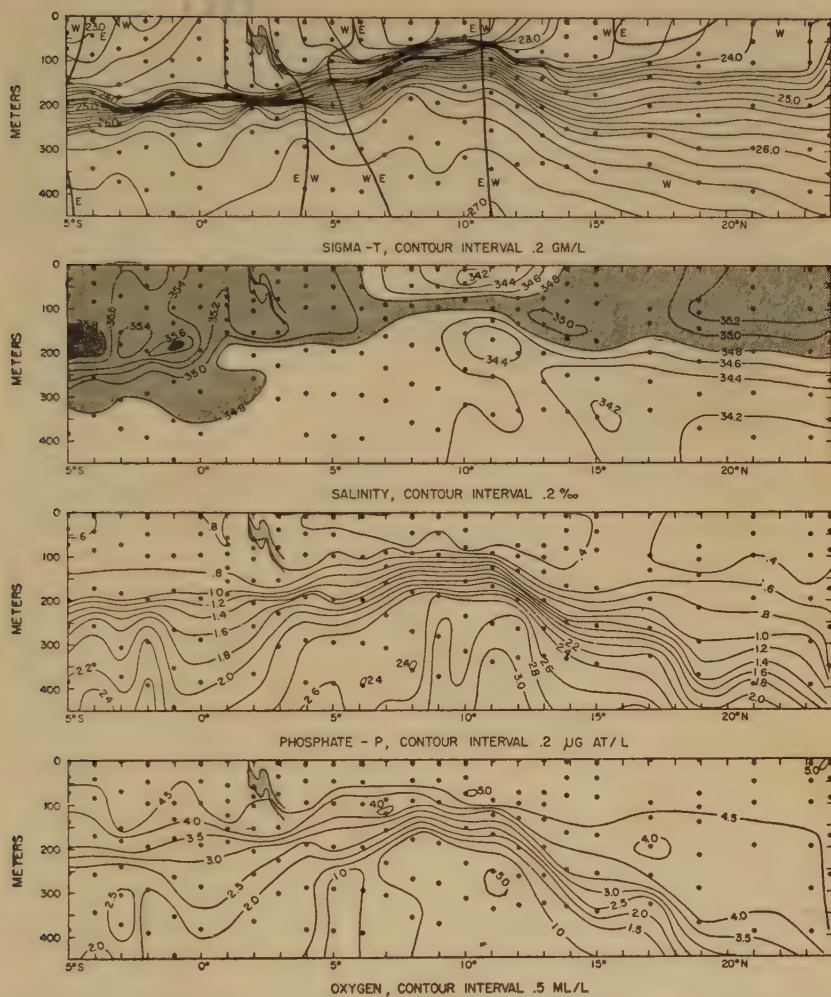


Figure 2. Cross sections of σ_t , salinity, inorganic phosphate, and dissolved oxygen along primarily 172° W (see Fig. 1) based on observations by the M/V HUGH M. SMITH, January 26-February 8, 1950. Dots indicate positions of observations. Shaded zone in surface layer is a front. Boundaries between east-flowing (E) and west-flowing (W) currents, as determined by dynamic calculations, drawn on σ_t cross section outside the 3° parallels.

them. A case in point exists in the vicinity of the Countercurrent. Here tongues of high-salinity water pointing from the north and south are joined by a narrow neck of somewhat less saline water. This layer is one of maximum salinity in the vertical distribution, separating still fresher water below the thermocline from that in the surface layer.

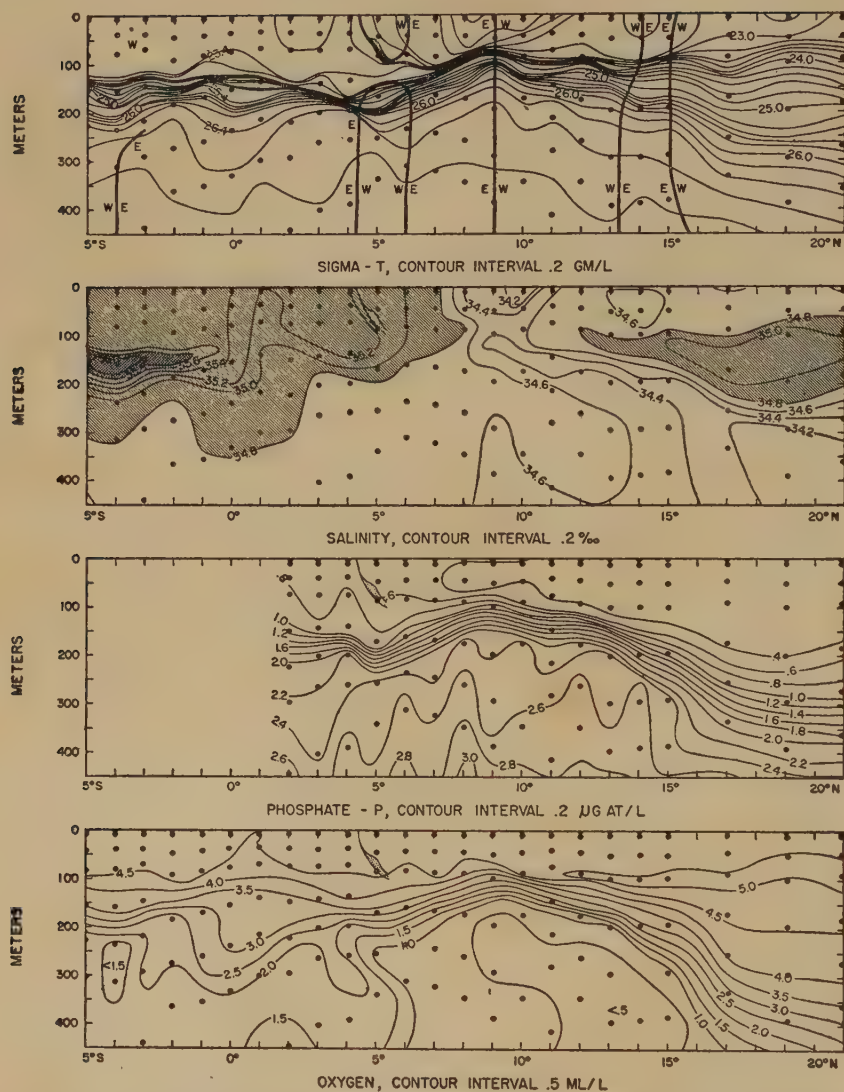


Figure 3. Cross sections of σ_t , salinity, inorganic phosphate, and dissolved oxygen along 158° W (see Fig. 1) based on observations by the M/V HUGH M. SMITH, July 28–August 6, 1950. Dots indicate positions of observations. Shaded zone in surface layer is a front. Boundaries between east-flowing (E) and west-flowing (W) currents, as determined by dynamic calculations, drawn on σ_t cross section outside the 3° parallels.

This distribution can be maintained by mixing processes alone, the loss of salt vertically by diffusion from the neck being balanced by a replenishment due to lateral mixing.

The saline layer in the upper part of the thermocline that originates far to the south of these sections (Defant, 1936) ends abruptly near the equator, giving the appearance of saline tongues in Figs. 2 and 3 (albeit somewhat less clear-cut in the former figure). Whether this saline layer extends to the equator by virtue of a current or lateral mixing cannot be demonstrated here, but its abrupt termination near the equator is consistent with upwelling. The high-salinity water in the upper part of the thermocline that is carried upward by upwelling will be mixed with waters of the turbulent surface layer, and the saline layer mixed away.

There is no evidence of significant upward motion anywhere along the sections except near the equator. In general the surface layer consists of warm light water of low inorganic phosphate concentration, characteristic of water that has been near the surface for a considerable time. The σ_t surfaces are not so oriented that flow along them could renew the surface layer, as can occur near the equator.

In particular, there is no evidence to support the suggestion by Defant (1936) and Sverdrup, et al. (1942) that there is upwelling at the boundary between the North Equatorial Current and the Countercurrent. Although more than one east-flowing current is indicated on the σ_t sections, the dynamic calculations indicate a major countercurrent with its northern boundary near $10\frac{1}{2}^\circ$ N and 9° N, shown respectively on Figs. 2 and 3. The thermocline is relatively near the sea surface along this boundary because of the "geostrophic effect," i. e., because of the dynamics of a steady current in the northern hemisphere which requires that dense water be found along the left boundary. It does not follow, of course, that upwelling is occurring or that it need occur at all to maintain this mass distribution. Because of the shallow position of the thermocline along this zone, however, nutrient-rich water may on occasion reach the surface as a result of wind stirring or through the direct absorption of radiant energy, which would allow upward motion across σ_t surfaces. Occurrences of the former would be sporadic, during excessive winds, and upward motion due to the latter would be slow, since little radiation penetrates to the thermocline. Probably neither process is of comparable importance to that of upwelling in adding nutrients to the surface layer in the central Pacific. Our hydrographic cruises have revealed that the surface layer near the Countercurrent boundary is nutrient-poor (Figs. 2 and 3).

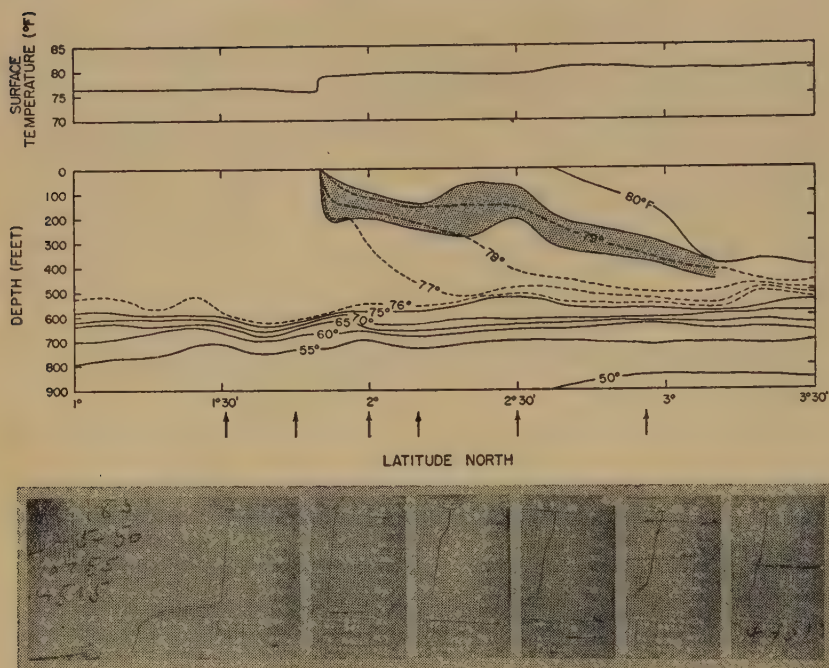


Figure 4. Thermal structure of the Equatorial Front at 172° W on February 5, 1950. Uppermost curve is surface temperature showing frontal discontinuity at $1^{\circ} 50'$ N (also see Fig. 5). Middle diagram, showing subsurface thermal structure, is an enlarged view of a small part of the cross section of Fig. 2. The frontal zone is shaded. Note that the vertical exaggeration ($\div 300 : 1$) gives rise to an apparent thickening of the frontal zone below the sea surface. The arrows indicate positions of the six BTs which are reproduced in the lower part of the figure.

HORIZONTAL CONVERGENCE AND SINKING

On several occasions (including the station lines on which Figs. 2 and 3 are based) our vessels crossed a pronounced oceanic convergence or front near the equator. In Figs. 2 and 3 this Equatorial Front appears as a shaded zone in the surface layer just north of the equator. It does not occur at the boundary between the Countercurrent and the South Equatorial Current. The thermal structure of the front that appears in Fig. 2 is shown in detail in Fig. 4. It is well defined by the continuous horizontal and vertical temperature records. North of its intersection with the sea surface it is revealed by BTs as a stable zone within the surface layer. The actual surface thermograph record, showing a near discontinuity at the front, is reproduced as Fig. 5.

Besides the front that appears in Fig. 3, there were indications of a second front at about $1^{\circ} 45'$ N, between the pocket of relatively low

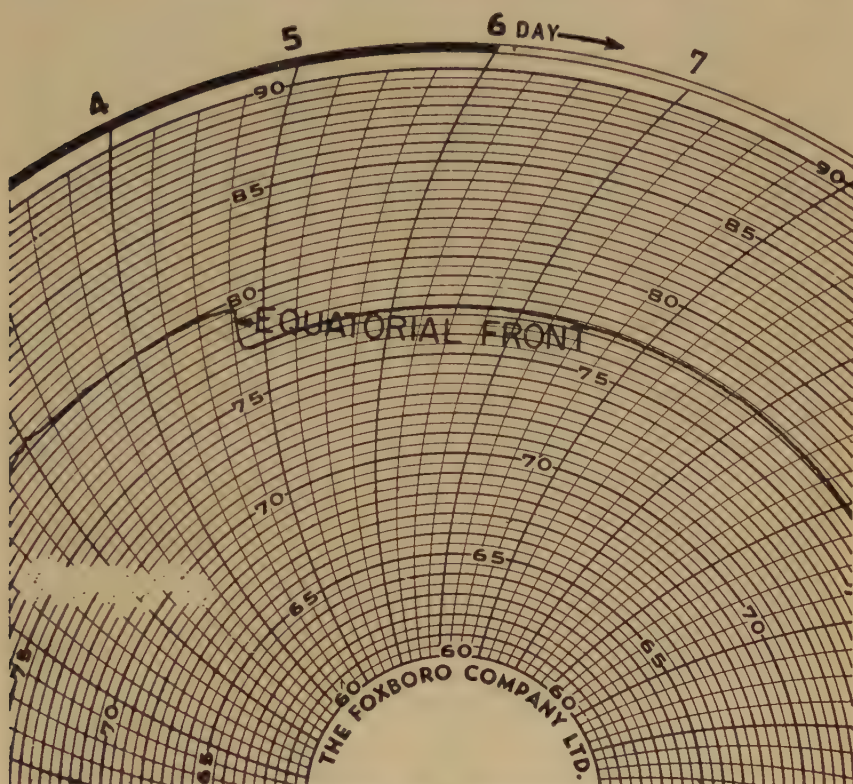


Figure 5. Thermograph trace showing near discontinuity at the Equatorial Front at 4:47 p. m., L. S. T., February 5, 1950.

density water near $2-3^{\circ}$ N and the dense water centered near the equator. The second front is not drawn because it is barely discernible in the BTs.

How the front is formed is not known, but the maintenance of such an intense temperature gradient indicates a continuous renewal of the water types on one or both sides of the front.

The BTs in Fig. 4 show striking homogeneity in the dense water immediately south of the front. Vertical turbulence would be virtually unimpeded in this water, and there is evidence to support the thesis that such turbulence is actually going on. For example, the BT traces show a sharp "corner" at the bottom boundary of the homogeneous surface layer. This characteristic of the trace along with the concentration of gradient in the upper part of the thermocline would be eliminated were it not maintained by some active process, presumably by turbulence.

The existence of this homogeneous region suggests that some water that sinks beneath the front returns equatorward in the lower part of the surface layer. This would complete a cellular circulation in the meridional plane, with ascending flow near the equator, sinking near the front, surface flow towards the front, and equatorward flow below. Disregarding the effects of external factors which act to alter the density within the cell, the latter can exist only in homogeneous water and still be consistent with principles of isentropic flow.

Although a distinct Equatorial Front is not common in the central Pacific, the thermal structure of the surface layer near the equator is usually complex, indicating the simultaneous existence of possibly two or three indistinct fronts, in the process of formation or dissipation.

When the Equatorial Front is not present there seems to be no way of demonstrating convincingly with cross sections that sinking is or is not occurring. There is some theoretical basis for expecting horizontal convergence and sinking north of the equator during southeast tradewinds, and this will be discussed later.

QUALITATIVE THEORETICAL CONSIDERATIONS

The complete hydrodynamic expression for horizontal motion equates the acceleration to the vector sum of the horizontal components of the following:

- (1) the Coriolis force (the deflecting force due to the earth's rotation) per unit mass,
- (2) the pressure-gradient force per unit mass,
- (3) the frictional force (resulting from viscous and eddy stresses within the ocean and the wind stress at the sea surface) per unit mass.

Ekman (1905), who described in detail the current that would be produced in a deep, homogeneous, unbounded ocean by a wind stress at the sea surface, assumed that this stress is balanced entirely by the horizontal component of the Coriolis force. The steady-state transport of this "wind drift current" is directed one right angle *cum sole* from the wind direction (i. e., to the right of the wind direction in the northern hemisphere, to the left of the wind direction in the southern hemisphere). For a given wind stress the magnitude of the current is inversely proportional to the sine of the latitude. Thus, a given wind stress directed west will produce a smaller poleward transport at a high latitude than it would at some position nearer the equator. This is an important feature of convergence in the region of northeast trades, as discussed by Montgomery (1936). Weenink and Groen (1952) have stated that friction may be neglected in computing cur-

rents outside latitude “. . . 2 or 3 degrees . . .”. Thus convergence of the type described by Montgomery may be significant as near to the equator as 2 or 3 degrees latitude.

Neumann (1947), basing his argument on the concept of the wind drift current, has pointed out that convergence should occur along the northern edge of the belt of southeast tradewinds where the wind speed drops off toward the doldrums region.

Ekman's model cannot approximate conditions near the equator where the deflecting force is negligibly small; for the ensuing discussion, therefore, the equatorward limit of application of this model will be set at the 3° parallels in accordance with the work of Weenink and Groen. If the frictional force that acts to retard the current is incorporated into Ekman's wind drift concept, it is possible to discuss a model circulation that is meaningful in a low latitude. Since the magnitude of the retarding frictional force, and hence the magnitude of this current transport, is uncertain, the discussion will be limited to a few qualitative remarks.

Fig. 6 illustrates the steady-state transports that will occur near the equator and away from the effect of boundaries, if only the frictional and deflecting forces are considered. The transport magnitude is drawn constant. In addition to vectors representing the transport that occurs with each wind direction, the meridional components are included in Fig. 6 to emphasize the regions of convergence and divergence. For example, if the wind is steady and uniform from the east, the current in a band along the equator will be meridionally divergent. Immediately at the equator, where there is no deflecting force and since we are assuming no pressure gradient, the transport of the current is in the direction of the wind. Poleward of 3° , Ekman's wind drift model applies and the steady-state transport is at right angles to the wind in both hemispheres, directed away from the equator. Between the equator and 3° there is a gradual change of direction of the current transport. The flow is strongly divergent. Thus, with a steady east wind along the equator, and under the special conditions described, there is a divergent current.

During a wind from the west, the steady-state transport of the wind drift current outside the region between the 3° parallels is directed toward the equator. The flow is strongly convergent. If the wind blows from the south, these same considerations lead to parallel zones of divergent flow (south of the equator) and convergent flow (north of the equator). There is a transport of water across the equator toward the north. During a wind from the north the divergent and convergent zones are interchanged and the transport at the equator is toward the south.

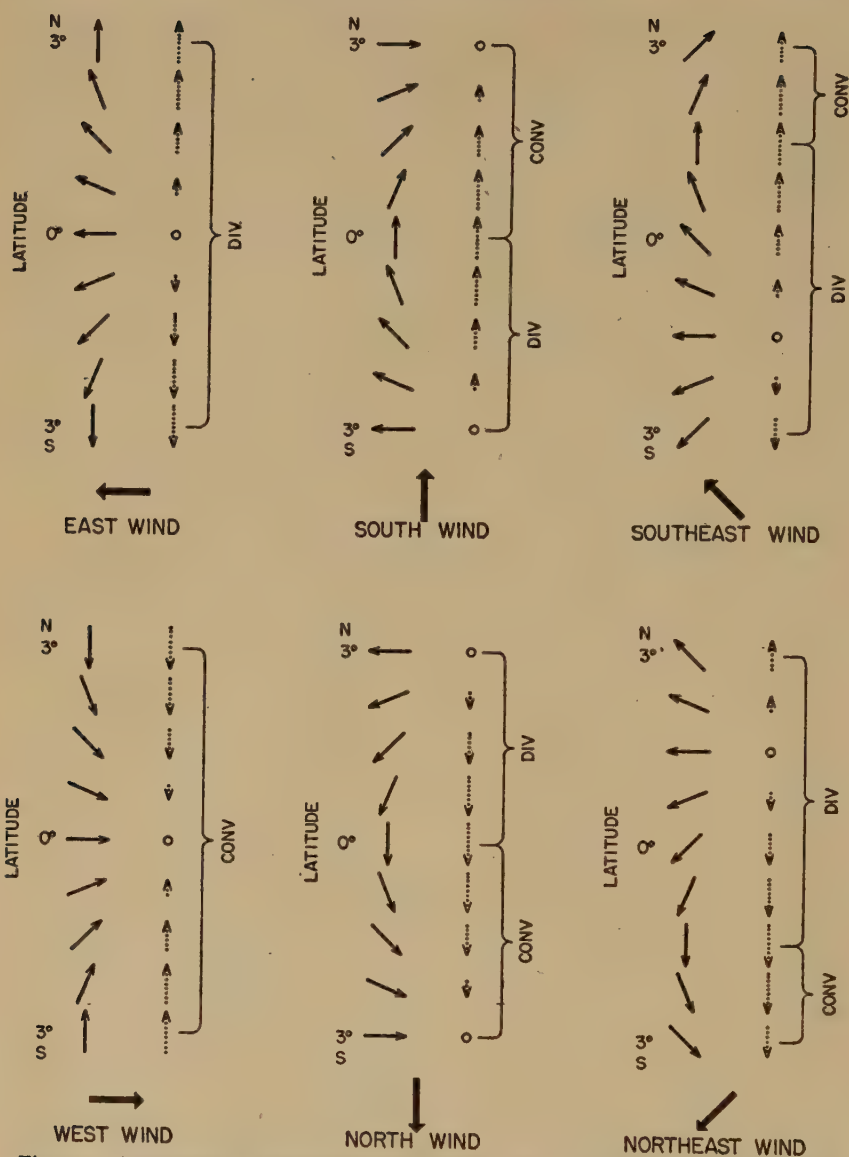


Figure 6. Directions of current transport (solid arrows) which would exist near the equator under various wind conditions if there were no pressure-gradient force acting. The current magnitude is drawn everywhere constant (solid arrows). For each wind condition the meridional components of the current transport (dotted arrows) are drawn to emphasize the regions of meridional divergence (Div.) and convergence (Conv.).

Southeast trades blow over a large part of the equatorial Pacific throughout the year. Under conditions of the model during a southeast wind, there is convergence in a narrow band near $2-3^{\circ}$ N, with divergence to the south as indicated in Fig. 6.

Since the pressure gradient has not been considered in the discussion leading to the divergence and convergence features of Fig. 6, it should be expected that these features will never be found exactly as described in the real ocean. In the real ocean, which is bounded and over which the prevailing wind velocity varies in space, a pressure-gradient force develops when the wind has blown for a sufficient length of time. Apparently this pressure-gradient force reduces the angle between wind direction and current-transport direction to less than a right angle. For example, the current transport chart of the North Pacific (Sverdrup, et al., 1942; 727, fig. 205) shows that there is rather close agreement in transport directions with directions shown on charts of predominant winds. Thus, it seems that the actual transport of the current usually is not directed a full right angle from the wind direction.

Nevertheless, vertical motion can occur even though the extreme divergence and convergence associated with the steady-state situations diagramed in Fig. 6 are never reached. Thus upward flow can be induced by divergence resulting from only a slight turning of the current *cum sole* from the wind direction. Similarly, convergence and divergence zones will exist as drawn for north and south winds if the current deviates only slightly from the wind direction. However, the convergence indicated during a southeast wind depends on the existence of a current directed north at some latitude, north of which the meridional component of the current decreases because of a further turning of the total current *cum sole*. Since the pressure-gradient force generally reduces the angle between current transport and wind direction to considerably less than a right angle, the convergence which appears in Fig. 6 for a southeast wind will probably not be found in the real ocean.

The divergence feature of the model in Fig. 6 seems to explain the upwelling which is apparent near the equator. The convergence feature is probably of importance in the real ocean when a wind is from the west or when the "southeast" trades back nearly to south. However, convergence north of the equator is expected during southeast tradewinds due to the deceleration of wind speed which occurs near the doldrums and due to the convergence of the wind drift current.

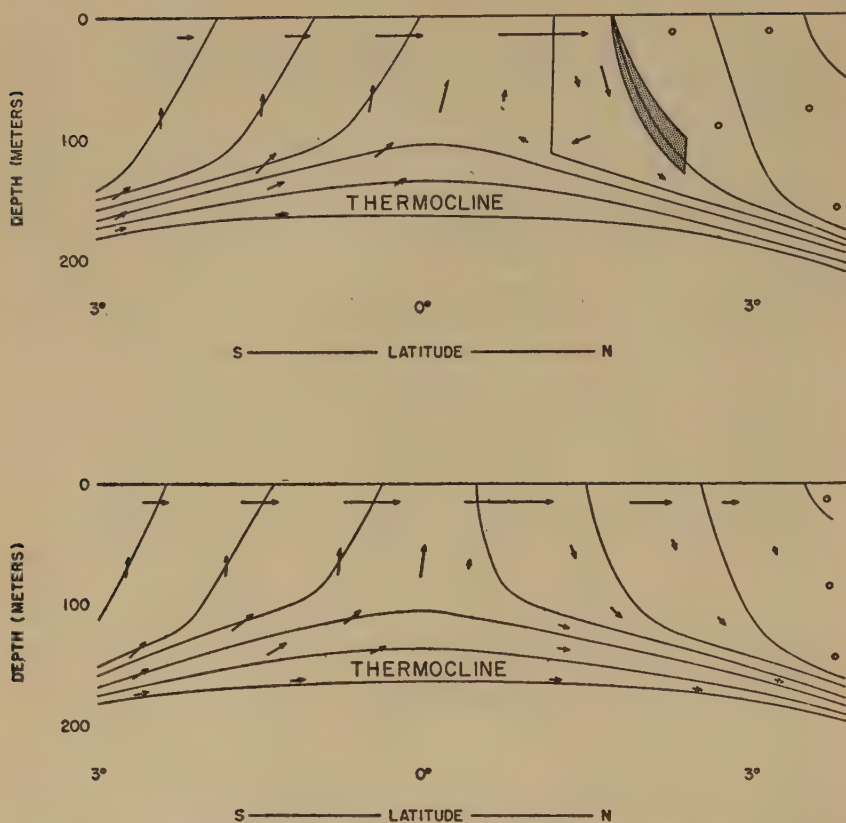


Figure 7. Schematic representation of circulation in the meridional plane near the equator during a southeast wind when front is present (*above*) and when no front is present (*below*). Full lines indicate surfaces of constant σ_t . The arrows have the character of streamlines and do not represent trajectories. The arrow shaft lengths indicate roughly the relative magnitudes of flow. Small circles indicate regions of slight and variable flow in this plane.

THE MERIDIONAL CIRCULATION

Fig. 7 presents schematically the meridional circulation which appears to prevail during a steady southeast wind. The full lines represent constant σ_t and are intended to be stationary in the two parts of the figure. The arrows have the character of streamlines and do not indicate trajectories. There are, of course, strong zonal currents.

The surface water moves with a component northward under the influence of southeast trades. Horizontal divergence near the equator induces upwelling. The current near the surface can cross σ_t surfaces toward greater density by virtue of an increase in the current's density

due to admixture of relatively dense water from below; this latter feature is indicated in the figure by arrows at mid-depth, shown crossing σ_t surfaces toward lower density.

The surface water of greatest density occurs at the equator. Here the water is cooler than that which would be in radiative equilibrium with incoming solar radiation that tends to increase temperature (and decrease density) at this latitude. Therefore, as the water moves northward its density is reduced by warming and it crosses σ_t surfaces toward lower density. Horizontal convergence occurs north of the equator during southeast tradewinds. Continuity is maintained partly by sinking along σ_t surfaces.

On some occasions the northward current is blocked by an Equatorial Front, shown as a shaded zone in the upper diagram of Fig. 7. On such occasions some of the water in the lower part of the surface layer returns equatorward. In a region of persistent northeast winds across the equator, one would expect a meridional circulation similar to that appearing in Fig. 7, mirrored in the equatorial plane.

INFLUENCE OF CIRCULATION ON ZOOPLANKTON DISTRIBUTION

Graham (1941), using CARNEGIE data, has shown a high plankton population near the equator which he attributes to upwelling. Our results are in good agreement with this idea (King and Demond, MS). The plant and animal life that is dependent on the meridional circulation just described should exhibit certain additional features in its distribution.

Following the introduction of nutrients into the euphotic zone, e. g., by upwelling near the equator, phytoplankton and then zooplankton would be expected to increase. If the current near the equator has a northward component, as during southeast tradewinds, the plankton will be displaced northward. In general the maximum zooplankton concentration would be expected somewhere between the region of nutrient enrichment and the zone of horizontal convergence, the magnitude of the displacement northward being dependent on the time rate of zooplankton increase relative to the rate of flow northward. If this flow is relatively rapid the zooplankton may be carried to the zone of horizontal convergence north of the equator or, if a front exists, to the convergent zone south of the front. Due to its ability of directed vertical swimming, the motile zooplankton can maintain its level against the slight downward flow associated with horizontal convergence and will tend to concentrate in the convergent zone.

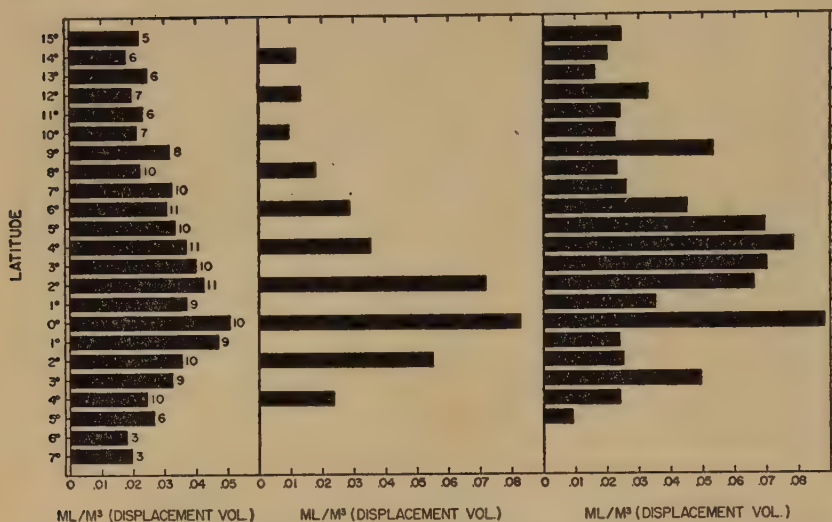


Figure 8. LEFT: Zooplankton data from 11 crossings of the equatorial currents between the 140° W and 180th meridians, combined grossly without regard for longitude or season. The number of observations included in the averaging for each degree of latitude appear at the right. MIDDLE AND RIGHT: Zooplankton data concurrent with the hydrographic sections of Figs. 2 and 3, respectively.

King and Demond (MS) have reported zooplankton results from the central Pacific. The left histogram of Fig. 8 showing the meridional variation in zooplankton abundance is based on data collected during 11 crossings of the equator between 140° W and the 180th meridian, a region over which southeast tradewinds predominate. All of these samples were taken with oblique hauls down to 200 m with nets having a body of 30XXX grit gauze and cod end of 56XXX grit gauze. The diagram includes data collected during each season. Apparently the maximum zooplankton concentration is related to the equatorial upwelling. Although the peak abundance occurs at the equator, the bulk of the plankton is displaced a little toward the north, which is consistent with the proposed meridional circulation.

The middle and right histograms of Fig. 8 are based on net hauls made concurrently with the hydrographic stations on which Figs. 2 and 3 are based. These distributions seem to show the influence of a circulation like that shown in the upper diagram of Fig. 7. The former indicates a rather abrupt decrease in zooplankton abundance northward across the front. The latter shows the zooplankton concentrated near the front.

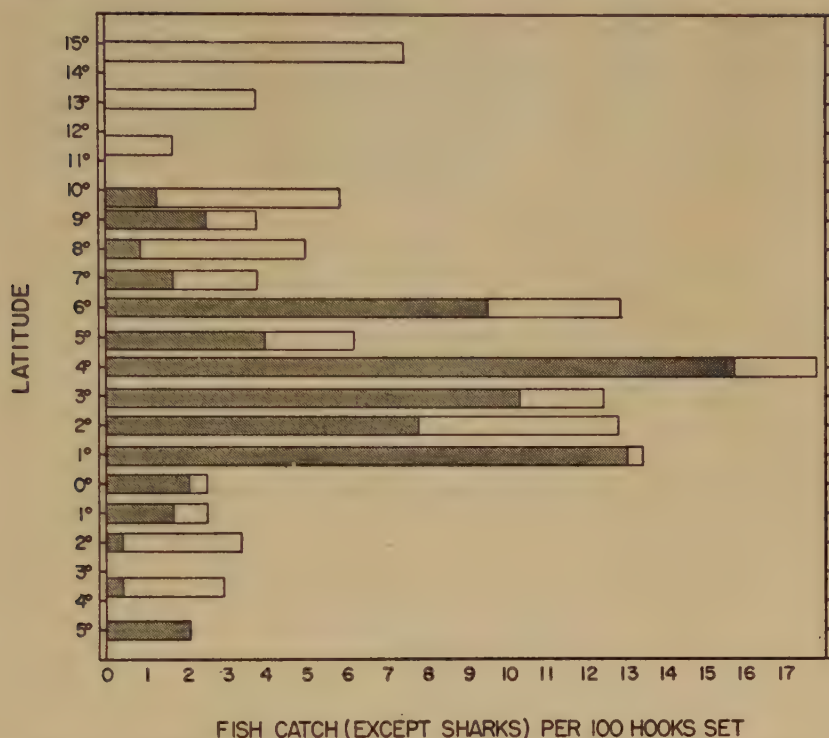


Figure 9. Abundance of large fish (except sharks) along 150° W Long. as indicated by catching rate during SMITH cruise 11 across the equatorial currents. Shaded portion represents proportion of catching rate due to yellowfin tuna (*Neothunnus macropterus*) alone.

RELATED FISH DISTRIBUTION

An integral part of our program has been to relate the circulation to the distribution of large fishes. Systematic sampling of these fishes, principally of tunas, has been described in detail by Murphy and Shomura (MS).

The results of a series of fishing stations along 150° W during August–October 1951 are shown in Fig. 9. Although complete hydrographic observations could not be taken during the fishing, the thermograph records show that there was no significant front. The circulation was probably that which arises with southeast tradewinds which, according to the pilot charts, predominate near the equator during these months.

The striking abundance of large fish, particularly of yellowfin tuna (*Neothunnus macropterus*), north of the upwelling suggests a causal

relationship to the circulation described in this paper. However, subsequent cruises have shown that the fish distribution sometimes is less clearly related to the circulation. Of course the fish distribution depends on a complex of factors, many of which are not considered here. Generally, however, in that part of the central Pacific over which southeast tradewinds blow, the greatest catches occur north of the equator in the region of convergence.

SUMMARY

1. Two sets of meridional sections showing the distributions of density (σ_t), salinity, inorganic phosphate, and dissolved oxygen across the equatorial currents of the central Pacific have been presented and are discussed briefly.

2. The sections show clearly the well known equatorial upwelling, but they do not support the thesis that upwelling is occurring at the northern boundary of the Equatorial Countercurrent.

3. An Equatorial Front, separating dense upwelled water near the equator from water of lesser density found generally in the surface layer of the South Equatorial Current, is described. Horizontal convergence and sinking are apparently associated with this front. The front does not coincide with the boundary of the Equatorial Countercurrent.

4. Reasons have been advanced for the existence of convergence north of the equator during southeast tradewinds when no front exists.

5. By modifying Ekman's theory of the "wind drift current" to include the total effect of friction, it is possible to discuss qualitatively a model that applies at and near the equator. In terms of this model it has been shown that there is a zone of horizontal divergence and an adjacent zone of convergence near the equator. The boundary between meridionally convergent and divergent flows shifts latitudinally and is dependent upon the wind direction. The divergence feature of this model seems to explain the equatorial upwelling. The convergence may at times produce significant sinking.

6. The circulation in a meridional plane across the equator during southeast tradewinds is summarized in Fig. 7.

7. The distribution of zooplankton and tunas in the central Pacific suggests a strong influence by the meridional circulation described.

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ON THE ANTARCTIC CIRCUMPOLAR CURRENT¹

By

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ABSTRACT

In 1951 Munk and Palmén discussed the dynamics of the Antarctic Circumpolar Current and found that they could explain the total mass transport of this current by assuming a far larger value for the coefficient of lateral mixing than had been obtained for other parts of the oceans. An attempt to solve the same problem in terms of the current velocity itself reveals that the slope of the sea surface and the vertical distribution of current velocity could be satisfactorily explained if the very high value which had been anticipated by Munk and Palmén were assumed for the lateral mixing coefficient. It was found also that the distributions of surface slope and velocity are not practically influenced by lateral mixing and are inconsistent with actual observations so long as the coefficient of lateral mixing remains less than $10^6 \text{ g cm}^{-1} \text{ sec}^{-1}$.

INTRODUCTION

In 1951 Munk and Palmén published a paper on the dynamics of the Antarctic Circumpolar Current in which they showed that the mass transport in the Antarctic Ocean is inversely proportional to the coefficient of horizontal mixing and that the computed transport is one hundred times that observed. They attributed the discrepancy between the computed and observed values to the effect of submarine ridges, and therefore they suggested that appreciable motion must occur at the bottom.

The conclusion that in a zonal ocean the mass transport produced by a planetary wind system is inversely proportional to the coefficient of horizontal mixing confirms a result previously obtained by Hidaka (1950). He found that a value of $10^6 \text{ g cm}^{-1} \text{ sec}^{-1}$ for the horizontal mixing coefficient is most plausible for explaining the actual surface slope of the ocean. Since both of these papers employ mass transport as the dependent variable, neither one allows a determination of the vertical velocity distribution. Recently Hidaka and Takano (1952) solved the problem in terms of the current velocity itself.

In the present paper, a similar solution in terms of the current velocity is applied to the Antarctic Circumpolar Current; and the

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pattern of water movement in the Antarctic Ocean, particularly with reference to the influence of horizontal mixing, is studied.

THEORY

Taking x - and y -axis positive eastward and northward respectively and z -axis vertically downward, the equations of motion are

$$\begin{aligned}\frac{A_v}{\rho} \frac{\partial^2 u}{\partial z^2} + \frac{A_h}{\rho} \left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2} \right) + 2\omega \sin \phi \cdot v &= \frac{1}{\rho} \frac{\partial p}{\partial x}, \\ \frac{A_v}{\rho} \frac{\partial^2 v}{\partial z^2} + \frac{A_h}{\rho} \left(\frac{\partial^2 v}{\partial x^2} + \frac{\partial^2 v}{\partial y^2} \right) - 2\omega \sin \phi \cdot u &= \frac{1}{\rho} \frac{\partial p}{\partial y},\end{aligned}$$

where u, v are the components of the current velocity in x - and y -directions, ρ the density, p the pressure, A_h and A_v the coefficients of horizontal and vertical mixing, ω the angular velocity of the earth, and ϕ the geographical latitude.

If we assume that the prevailing winds blow in the E-W direction only, u, v, p and the surface elevation ζ will be independent of x . In this case, putting $W = u + iv$, the above equations may be combined as follows:

$$\frac{A_v}{\rho} \frac{\partial^2 W}{\partial z^2} + \frac{A_h}{\rho} \frac{\partial^2 W}{\partial y^2} - 2\omega i \sin \phi W = ig \frac{\partial \zeta}{\partial y}, \quad (1)$$

where g is the acceleration of gravity. The equation of continuity is

$$\frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0, \quad (2)$$

where w is the vertical component of velocity.

As boundary conditions, we have

$$W = 0 \quad \left\{ \begin{array}{l} \text{at } z = h \text{ (the bottom)} \\ \text{at } y = \pm l \text{ (45° S and 70° S)} \end{array} \right. \quad (3)$$

$$(4)$$

$$A_v \frac{\partial W}{\partial z} + \tau = 0 \text{ at } z = 0 \text{ (the surface)} \quad (5)$$

where τ is the wind stress in x -direction.

Now we write

$$W = \sum_{s=1}^{\infty} w_s(y) \cos \frac{(2s-1)\pi z}{2h}, \quad (6)$$

where

$$w_s(y) = \frac{2}{h} \int_0^h W(\lambda) \cos \frac{(2s-1)\pi \lambda}{2h} d\lambda, \quad (7)$$

and by Stokes' method we write

$$\frac{\partial^2 W}{\partial z^2} = \frac{2}{h} \sum_{s=1}^{\infty} \cos \frac{(2s-1)\pi z}{2h} \int_0^h \frac{\partial^2 W}{\partial \lambda^2} \cos \frac{(2s-1)\pi \lambda}{2h} d\lambda. \quad (8)$$

Using (3), (5), (7), we have

$$\frac{2}{h} \int_0^h \frac{\partial^2 W}{\partial \lambda^2} \cos \frac{(2s-1)\pi \lambda}{2h} d\lambda = \left[\frac{2}{h} \frac{\tau}{A_v} - \frac{(2s-1)^2 \pi^2}{4h^2} w_s(y) \right]; \quad (9)$$

then (8) becomes

$$\frac{\partial^2 W}{\partial z^2} = \sum_{s=1}^{\infty} \left[\frac{2}{h} \frac{\tau}{A_v} - \frac{(2s-1)^2 \pi^2}{4h^2} w_s(y) \right] \cos \frac{(2s-1)\pi z}{2h}. \quad (10)$$

Since $1 = \frac{4}{\pi} \sum_{s=1}^{\infty} \frac{(-1)^{s+1}}{(2s-1)} \cos \frac{(2s-1)\pi z}{2h}$, substitutions of (6) and

(10) into (1) give

$$\begin{aligned} A_h \frac{d^2 w_s}{dy^2} - \left(2\omega \rho i \sin \phi + \frac{(2s-1)^2 \pi^2}{4h^2} A v \right) w_s \\ = \frac{4}{\pi} \frac{(-1)^{s+1} \rho g i}{(2s-1)} \frac{\partial \zeta}{\partial y} - \frac{2}{h} \tau. \end{aligned} \quad (11)$$

Let

$$w_s(y) = \sum_{m=1}^{\infty} D_{ms} \sin \frac{m\pi(l+y)}{2l}, \quad (12)$$

$$\frac{d\zeta}{dy} = \sum_{m=1}^{\infty} p_m \sin \frac{m\pi(l+y)}{2l}, \quad (13)$$

$$\tau(y) = \sum_{m=1}^{\infty} \tau_m \sin \frac{m\pi(l+y)}{2l}, \quad (14)$$

and since

$$\sin \phi \sin \frac{m\pi(l+y)}{2l} = \sum_{j=1}^{\infty} E_m^j \sin \frac{j\pi(l+y)}{2l},$$

where

$$E_m^j = \begin{cases} \frac{l}{R} \sin \phi_0 \sin \frac{l}{R} \left[\frac{1}{\left(\frac{l}{R}\right)^2 - (m-j)^2 \frac{\pi^2}{4}} - \frac{1}{\left(\frac{l}{R}\right)^2 - (m+j)^2 \frac{\pi^2}{4}} \right] & \text{for } m+j: \text{ even,} \\ \frac{l}{R} \cos \phi_0 \cos \frac{l}{R} \left[\frac{1}{\left(\frac{l}{R}\right)^2 - (m-j)^2 \frac{\pi^2}{4}} - \frac{1}{\left(\frac{l}{R}\right)^2 - (m+j)^2 \frac{\pi^2}{4}} \right] & \text{for } m+j: \text{ odd,} \end{cases}$$

and ϕ_0 is the latitude of the origin and R is the radius of the earth, (11) then becomes

$$\begin{aligned} - \left(\frac{m^2 \pi^2}{4l^2} A_h + \frac{(2s-1)^2 \pi^2}{4h^2} A_v \right) D_{ms} - 2\omega i \rho \sum_j D_{js} E_j^m \\ = \frac{4(-1)^{s+1} \rho g i}{\pi (2s-1)} p_m - \frac{2}{h} \tau_m, \end{aligned} \quad (15)$$

$$\begin{aligned} m &= 1, 2, \dots \\ s &= 1, 2, \dots \end{aligned}$$

Solving equations (15), the values of D_{ms} are represented as polynomials of τ_m and p_m .

Now integration of (2) with respect to Z gives

$$\int_0^h v dz = 0. \quad (16)$$

From (16), the values of p_m are determined as functions of τ_m so D_{ms} can be represented by τ_m only.

Then, from (6) and (12), the current velocity is given by

$$W = \sum_{m,s} D_{ms} \sin \frac{m\pi(l+y)}{2l} \cos \frac{(2s-1)\pi z}{2h}. \quad (17)$$

NUMERICAL COMPUTATIONS

We assume that the density is constant throughout the sea water and equal to 1, and that $\tau = 2$ dyne cm^{-2} ; then

$$\begin{aligned} \tau_1 &= 2.546, & \tau_2 &= 0, \\ \tau_3 &= 0.849, & \tau_4 &= 0, \\ \tau_5 &= 0.509, & \tau_6 &= 0, \\ &\dots & &\dots \end{aligned}$$

With $\omega = 7.29 \times 10^{-5} \text{sec}^{-1}$, $g = 980 \text{ cm sec}^{-2}$, $h = 4000 \text{ m}$, $A_v = 2 \times 10^3 \text{g cm}^{-1} \text{sec}^{-1}$, $A_h = 10^8 \text{g cm}^{-1} \text{sec}^{-1}$, the values of D_{ms} , when m and s are less than 6 and 8 respectively, are computed and shown in Table I. Here practical computations E_m^j other than E_m^{m-1} , E_m^m , E_m^{m+1} can be neglected.

The surface elevation is given by

$$\zeta = -1202 \cos \frac{\pi(l+y)}{2l} - 32 \cos \frac{2\pi(l+y)}{2l} - 79 \cos \frac{3\pi(l+y)}{2l} - 17 \cos \frac{5\pi(l+y)}{2l},$$

and the total mass transport M is given by

$$M = \int_{-l}^l \int_0^h \rho u dy dz = 8.1 \times 10^{15} \text{g sec}^{-1}.$$

Similarly, for $A_h = 10^{10} \text{g cm}^{-1} \text{sec}^{-1}$ computations are made. The values of D_{ms} are given in Table II. And the surface elevation and the total mass transport are as given by

$$\zeta = -148 \cos \frac{\pi(l+y)}{2l} - 3.9 \cos \frac{2\pi(l+y)}{2l} - 2.0 \cos \frac{3\pi(l+y)}{2l},$$

$$M = 9.3 \times 10^{14} \text{g sec}^{-1}.$$

In both cases we assume $A_v = 2 \times 10^3 \text{g cm}^{-1} \text{sec}^{-1}$, although this value is a little larger than that of other oceans. The magnitude of A_v , however, is not very important in numerical computations. Further, when A_h is less than $10^8 \text{g cm}^{-1} \text{sec}^{-1}$, the computed values are scarcely affected by its variation.

TABLE I. VALUES OF D_{ms} FOR $A_h = 10^8 \text{G CM}^{-1} \text{SEC}^{-1}$

s/m	1	2	3	4	5	6
1	138.3 + .28i	-1.00 - .02i	27.49 + .08i	.00 - .01i	9.92 + .04i	-.01 + .00i
2	-46.08 + .43i	.24 - .03i	-9.16 + .14i	.01 - .01i	-3.31 + .08i	.00 + .00i
3	27.64 + .15i	-.17 - .01i	5.48 + .07i	-.01 - .01i	1.98 + .05i	.00 + .00i
4	-19.79 + .57i	.18 - .04i	-3.93 + .16i	.00 - .01i	-1.42 + .08i	.02 + .00i
5	15.39 + .02i	-.09 + .00i	3.08 + .05i	-.01 - .01i	1.11 + .04i	.00 + .00i
6	-12.53 + .71i	-.06 - .05i	-2.53 + .19i	-.01 - .02i	-.91 + .10i	.00 + .00i
7	10.66 - .12i	.12 + .00i	2.09 + .02i	.00 - .01i	.76 + .02i	.00 - .02i
8	-9.20 + .85i	.09 - .06i	-1.79 + .21i	.00 + .01i	-.66 + .10i	.00 + .01i

TABLE II. VALUES OF D_{ms} FOR $A_h = 10^{10} \text{G CM}^{-1} \text{SEC}^{-1}$

s/m	1	2	3	4	5	6
1	16.97 + .15i	.01 - .01i	.68 + .05i	.01 - .01i	.16 + .02i	.00 + .00i
2	-5.67 + .40i	.00 - .03i	-.22 + .13i	-.01 - .01i	-.03 + .07i	.00 + .00i
3	3.40 + .27i	.00 - .02i	.14 + .10i	.00 - .01i	.05 + .05i	.00 + .00i
4	-2.41 + .38i	.01 - .03i	-.09 + .12i	-.01 - .01i	.00 + .07i	.00 + .00i
5	1.90 + .27i	.01 - .02i	.09 + .10i	.00 - .01i	.03 + .06i	.00 + .00i
6	-1.53 + .39i	.00 - .03i	-.05 + .12i	-.01 - .01i	.01 + .06i	.00 + .00i
7	1.32 + .26i	.00 - .02i	.06 + .10i	.03 - .01i	.03 + .06i	.00 + .00i
8	-1.11 + .39i	.00 - .03i	-.02 + .12i	-.04 - .01i	.01 + .06i	.00 + .00i

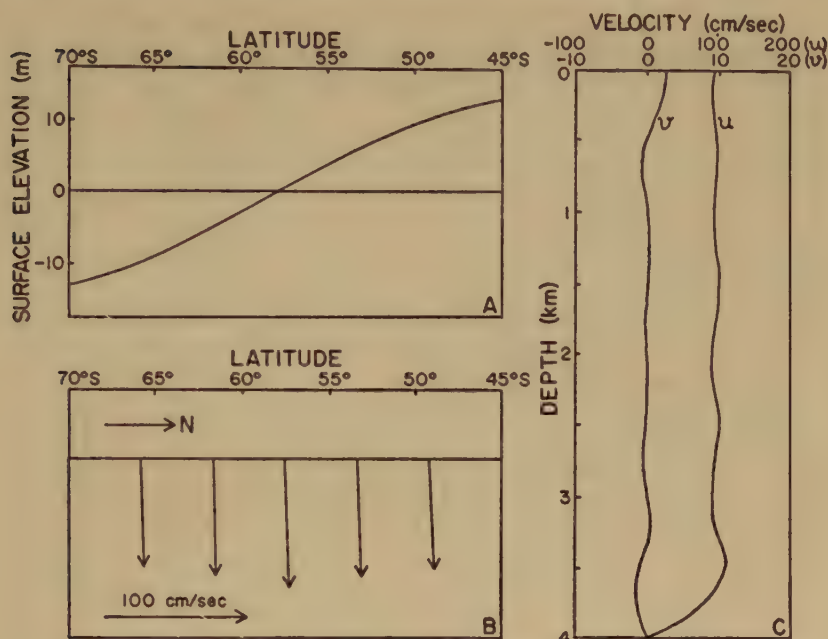


Figure 1. Wind current and surface elevation in the Antarctic ocean for $A_h = 10^8$ C. G. S. A. Surface elevation. B. Vector diagram of surface currents. C. Vertical distribution of the current velocity along the median line ($57^\circ 30' S$). u and v are taken positive eastward and northward respectively, and in fig. 1C the scale for v is magnified ten times that of u .

CONCLUSIONS

Summarizing the above computed results, the following conclusions are obtained.

(1) When the coefficient of horizontal mixing is less than $10^8 \text{ g cm}^{-1} \text{ sec}^{-1}$, the pattern of water movement is practically independent of the magnitude of A_h . This result agrees with that of Hidaka and Takano (1952).

(2) Total Mass Transport. The computed total mass transport is $8.1 \times 10^{15} \text{ g sec}^{-1}$ for $A_h = 10^8 \text{ g cm}^{-1} \text{ sec}^{-1}$ and $9.3 \times 10^{14} \text{ g sec}^{-1}$ for $A_h = 10^{10} \text{ g cm}^{-1} \text{ sec}^{-1}$. This is consistent with the result that the mass transport in a zonal ocean is inversely proportional to A_h (Hidaka, 1950; Munk and Palmén, 1951). The actual mass transport in the Antarctic Ocean is at least $1.5 \times 10^{14} \text{ g sec}^{-1}$. Even if we assume $A_h = 10^{10} \text{ g cm}^{-1} \text{ sec}^{-1}$, the computed value seems to be a little larger than that observed.

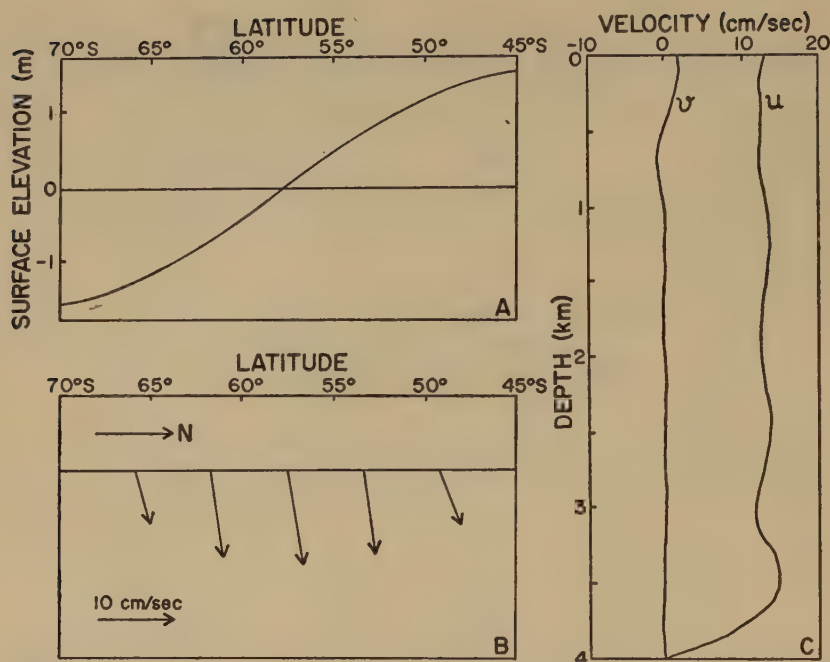


Figure 2. Wind current and surface elevation in the Antarctic ocean for $A_h = 10^{10}$ C. G. S. A. Surface elevation. B. Vector diagram of surface currents. C. Vertical distribution of the current velocity along the median line (57° 30' S). u and v are taken positive eastward and northward respectively.

(3) Surface Slope. In Figs. 1A and 2A, the surface slope is illustrated. Its range for $A_h = 10^8 \text{ g cm}^{-1} \text{ sec}^{-1}$ gives a large value of about 25 m, but for $A_h = 10^{10} \text{ g cm}^{-1} \text{ sec}^{-1}$ the range is only 3 m. Extrapolation of the surface slope into the Antarctic region, as given by Defant's chart of absolute topography, gives a value of about 2–3 m per 2000 km. Therefore the computed value of the slope for $A_h = 10^{10} \text{ g cm}^{-1} \text{ sec}^{-1}$ may be reasonable.

(4) Surface Current. In Figs. 1B and 2B, the surface currents are illustrated. For $A_h = 10^{10} \text{ g cm}^{-1} \text{ sec}^{-1}$ the directions and magnitudes of the currents are in good agreement with those observed.

(5) Vertical Distribution of the Current. The fact that the Antarctic Circumpolar Current reaches considerable depth has been pointed out by several authors. In 1941, Sverdrup discussed qualitatively the influence of the bottom topography on surface currents and explained that the Antarctic Circumpolar Current is sufficiently deep so that very sharp leftward deflections of surface currents are observed over deep submarine ridges near Drake Passage.

According to Figs. 1C and 2C, the meridional component of the current velocity is small compared with the E-W component and is nearly zero in depths of more than a few hundred meters. The E-W component is almost uniform from the surface down to the bottom. This result is consistent with the above-mentioned fact. The slight vertical fluctuations in the velocity of the E-W current come out from the fact that we adopted several terms only in the Fourier expansion in u .

From these results, if we assume $A_h = 10^{10} \text{ g cm}^{-1} \text{ sec}^{-1}$, the computed mass transport, the surface slope, as well as the current velocity and its vertical distribution are consistent with those observed, and the Antarctic Circumpolar Current may be explained without taking into account the effect of submarine ridges.

A value of $10^{10} \text{ g cm}^{-1} \text{ sec}^{-1}$ for the horizontal mixing coefficient is much larger than that obtained for other oceans. This coefficient, however, has ordinarily been defined as replacing the viscosity coefficients in the x - and y -components of the equations of motion when the motion is turbulent. In the present case we have solved these differential equations in conjunction with the equation of continuity and in accordance with the boundary conditions, and we have assigned a value to A_h which most plausibly explains the actual motion of the water. Therefore, so large a value may not be unnatural if we can affirm the existence of exceptionally great horizontal mixing in the Antarctic Region.

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A BATHYMETRIC PROFILE ACROSS THE HUDSON SUBMARINE CANYON AND ITS TRIBUTARIES¹

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ABSTRACT

Echo soundings recorded continuously during a crossing of the Hudson Submarine Canyon system 200 miles southeast of New York Harbor show that the tributaries in 1200–1800 fathoms depth differ in profile and gradient from the Hudson Canyon proper. Because the recordings are distorted by instrumentation, the true bottom configuration is computed by using Schuler's method. In the area studied, the main Hudson Canyon has a steep V-shaped profile whereas the major tributary has more gently sloping sides and a flat bottom. Of the two minor tributaries crossed, the short one has a broad valley profile, the long one a narrow profile. Differences between these canyons are attributed to the number and size of the mudflows and turbidity currents which stream down them.

INTRODUCTION

An extensive survey of the Hudson Submarine Canyon (5) has shown that the deepest gorges are cut in the upper 1200 fathoms of the continental slope and again on the continental rise from 1700 to 2100 fathoms depth (19). Observations show that the Canyon extends 200 miles further seaward than that observed by Veatch and Smith (20), has several tributaries entering at grade, and continues into 2650 fathoms before it spreads out in a delta on the floor of the North America Basin. No "hanging valleys," like those described in canyons off the California Coast (15), were found.

Subsequent study (4), (6), (7) has shown that great quantities of sand and shallow-water sediment have been transported down the Hudson Submarine Canyon system and have been deposited in a vast delta of coalescing fans at the Canyon's mouth. These sedimentary deposits are attributed to submarine turbidity currents which started on the unstable continental slope and continued out to sea. Such submarine erosion processes have been described (8), (12), and laboratory experiments (11) have shown that turbidity currents have the power to transport sediment and deposit it in graded layers. De-

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tailed topographic profiles of the Hudson Canyon and its tributaries were obtained with the Edo sonic sounder UQN1B recording on a greatly magnified scale (Fig. 1) along a traverse of the canyon area from 1600–1800 fathoms depth (Fig. 2).

Acknowledgment is made to Dr. E. T. Booth, Director of Hudson Laboratories, Columbia University, and to Drs. J. E. Nafé and R. A. Frosch, co-workers on the project. Discussions with B. C. Heezen have been extremely helpful.

METHOD

A continuous recording echo sounder, model UQN1B, manufactured by the Edo Corporation, College Point, Long Island, was used. Geographical positions were determined by hourly loran readings on two or more station pairs. Some canyon crossings were made with the instrument set on a scale of 0–6000 fathoms, a setting which gives no appreciable vertical exaggeration and obscures the smaller canyons. Other crossings were made with the instrument set on the 0–600 fathom scale; this same setting can be used also (Fig. 1) in 1200–1800 fathoms depth because the two pinging styli are mounted on a continuous moving belt so that the second stylus can record the first one's outgoing ping, thereby doubling the scale. (An additional pen mounted halfway between the two will record the returning echo for intermediate scales of 600–1200, 1800–2400, 3000–3600, and 4200–4800 fathoms.) With this arrangement a vertical exaggeration of about 10/1, depending on the ship's speed, is obtained. To the author's knowledge, recordings of this type were made previously by B. C. Heezen in 1952 on the ALBATROSS III and ATLANTIS, by the author on the KEVIN MORAN (7), and by the Scripps Institution of Oceanography.

This method of surveying brings out the minor irregularities in the ocean floor over a continuous track of varying width under the ship, but it records only the least depths within a cone of sound whose diameter varies with the type of instrument and the depth of water (1). For the instrument used in these observations, the half angle of the cone of sound is designated as 30° by the manufacturer, but in deep water the effective cone is much narrower.

To obtain an accurate configuration of an ocean bottom from such a large area of returning echoes, Schuler (14) has worked out a relation between the angle subtended by the cone of sound and the length of the returning echo. Schuler considers water depths up to 300 fathoms. In one case he uses the known angle of the cone of sound and computes the expected echo length; in a second case he determines the effective

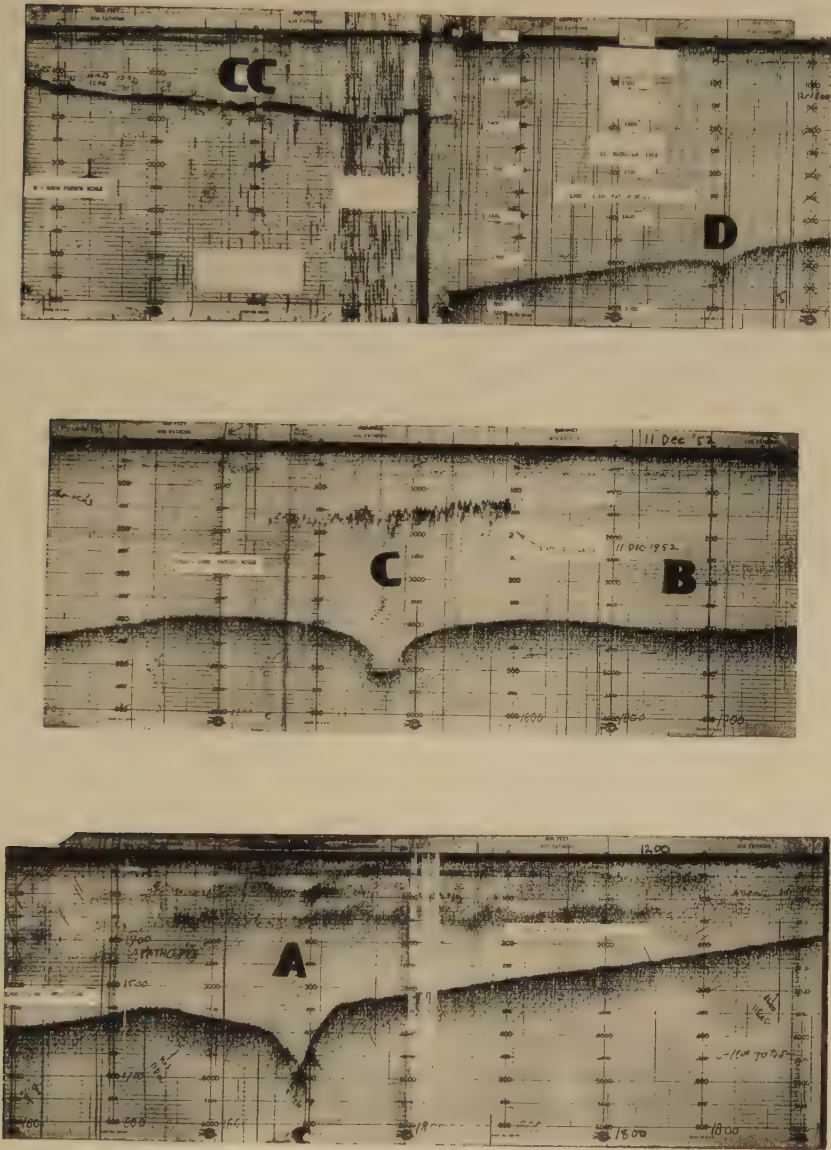


Figure 1. Echogram of the Hudson and some of its tributaries.

cone of sound from an observed echo length. Following suggestions by Dr. E. T. Booth, it was found that in much greater depths than those described by Schuler it is still possible to compute the effective cone of sound from a measurable echo length.

The area on the ocean floor from within which echoes are recorded on the instrument at a given gain setting can be computed from Schuler's equation: depth plus echo length = depth/cos ϕ , where ϕ is half the angle of the effective cone. Therefore, by measuring the depth and echo length from the record and by substituting these values in the equation, the effective cone of sound can be determined. For example, at *B* (Fig. 1) a depth of 1600 fathoms is indicated and the echo length is 50 fathoms. By substituting in the equation, $\phi = 14^\circ$; and by solving for the tangent ϕ , the diameter of the base of the effective cone at this depth and gain setting is 4800 feet.

In this analysis the width of the effective cone of sound is important because any difference in depth within the effective cone will be indicated as increased echo length on the record. As a declivity in the bottom is approached by the survey ship, the upper and lower boundaries of the trace will diverge.

Furthermore, these changes in the character of the trace will anticipate the survey ship by half the width of the effective cone. Thus the width of the flat-floored canyon is equal to the indicated width plus the radius of the effective cone of sound taken twice (Fig. 4). On the other hand, if the canyon is narrower than the effective radius, it will show not as an indentation on the record but only as a lengthening of the styli markings.

In order to solve Schuler's equation quantitatively, the recordings have to show considerable detail. For example, location *CC* is only two miles away from location *C* (Figs. 1 and 2). At *CC* the recorder was on the 6000 fathom scale and the Canyon is only barely discernable, whereas at *C* it was on the 600 fathom scale which brings out the flat floor and sloping sides of the Canyon.

HUDSON CANYON SYSTEM

The Hudson Canyon, a seaward extension of the Hudson Channel on the continental shelf, was mapped by early submarine physiographers (10), (17) and more recently by Veatch and Smith (20), who traced the Canyon out to 1200 fathoms. Its origin has been attributed to subaerial erosion, faulting, spring sapping, tsunamis, and more recently to turbidity currents. The arguments for or against these theses have been considered in detail by other workers (16), (18) and will not be examined here. However, the turbidity current is held by

some authors to be a most likely eroding agent. Daly (3) first attributed the submarine canyons to density currents formed in a time of lowered sea level. Recent geologic studies (4), (5), (6), (8), (9), (12), (13), (18) have brought out considerable evidence for a present-day environment on the continental shelf and slope which points to the action of mudflows and landslides which turn into turbidity currents. The characteristic V-shaped profile of the Hudson Canyon proper has led Kuenen (11) to think that this parent Canyon may have been developed by the Hudson River during the Pleistocene, a period of lower sea level, while the tributaries are due to later headward growth by turbidity currents which are still in operation.

The Hudson Canyon at *A* in Fig. 2 is shown to be a sharp V-shaped feature at *A* in Fig. 1 as compared with tributary *C* in Figs. 1 and 2. The indicated depth at the bottom of the V is 1670 fathoms. However, as the cone of sound moved across the Canyon it picked up echoes from both sides (Fig. 3) and thus made it appear shallower. This "crossover effect" is recognizable by the extending "tails" of the styli markings (*A* in Fig. 3) which meet at the true depth of the Canyon. The coalescing tails in *A* (Fig. 1) show the true depth of the Hudson Canyon to be 1715 fathoms, 200 fathoms below its banks. Sediment cored in the Canyon 20 miles downstream from this place and buried under 100 cm of gravel and foraminiferal clay contained pebbles up to 2 cm diameter (6) as well as shell fragments of the Pleistocene. This type of graded bedding in the Canyon floor, absent on its walls, indicates that the Canyon is the route of sediment transport by turbidity currents. The walls of the Canyon slope at 17° with the horizontal and are probably covered with the green pyritic clay that is so widespread in the region (4), (6).

Eight miles downstream the east wall of the Canyon is cut by tributary *B* (Figs. 1 and 2). Although this tributary was observed only five miles from where it joins the main Canyon "at grade" (19), it is a broad depression $2\frac{1}{2}$ miles wide with sides sloping only about 0.5° with the horizontal. There is no apparent further headward extension of this tributary, so it evidently has encroached from the 1800 fathom main Canyon depth to its present location by a series of mudflows or landslides that keep entering the main stream at grade.

Tributary *C*, also on the east wall of the Hudson Canyon, lies 14 miles downslope from *B* (Fig. 2). It has a flat bottom and is 120 fathoms deep (*C* of Fig. 1). The fathogram indicates that the flat floor of this canyon is $\frac{1}{2}$ mile wide, but distortion due to the effective cone of sound moving over the canyon's walls ahead of the ship has made it appear too narrow (Fig. 4). If the indicated width of the

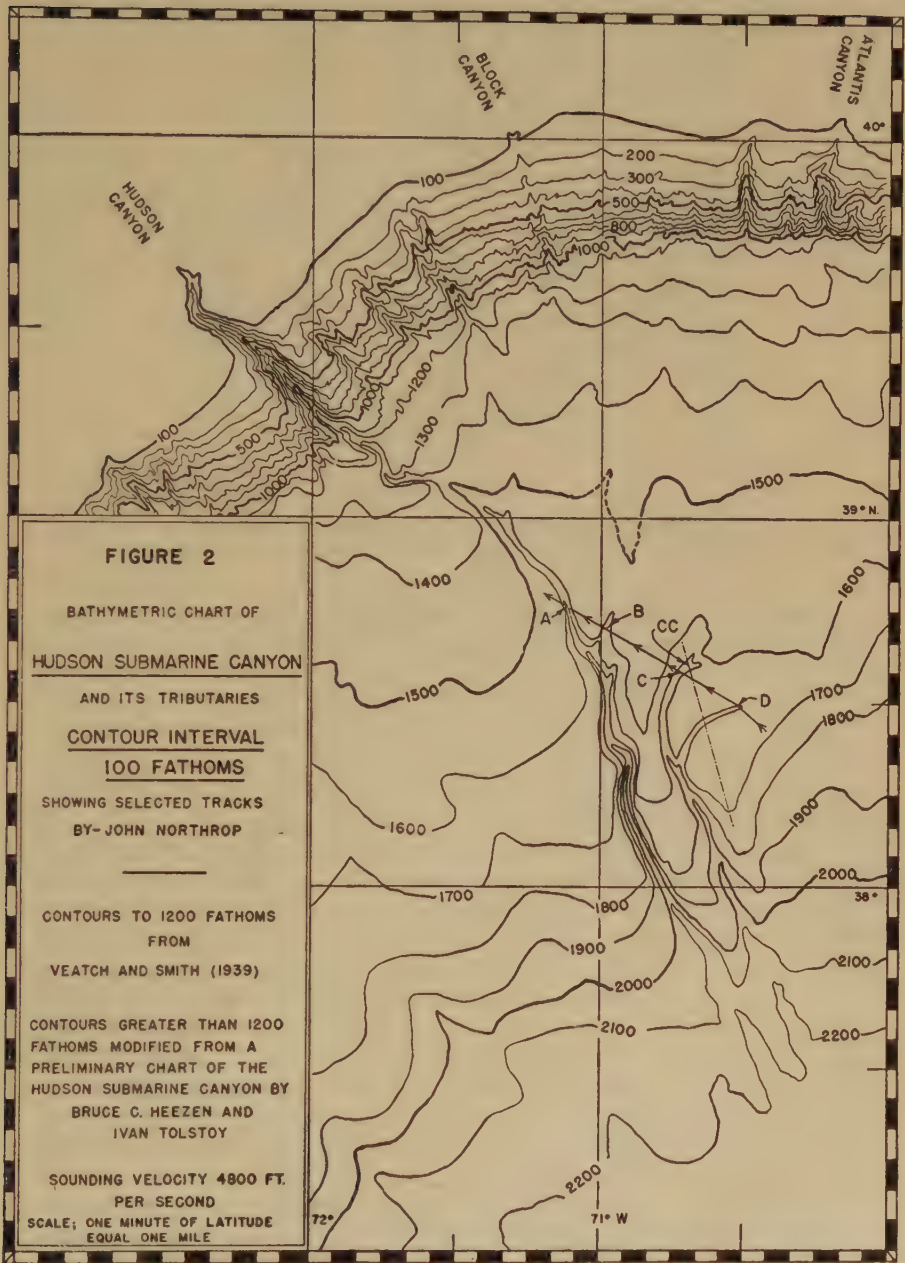


Figure 2. Index map showing the location of the profiles.

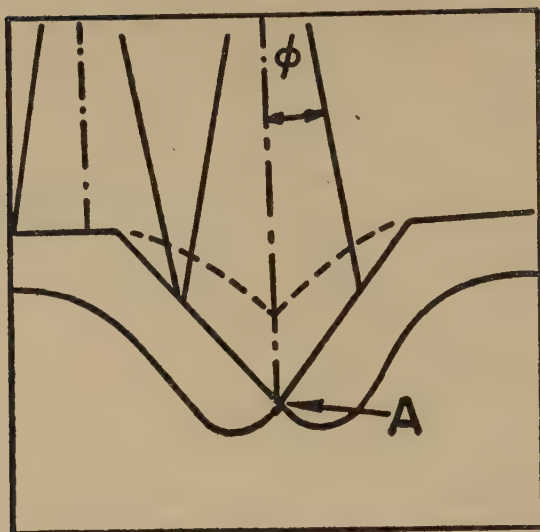


Figure 3. The crossover effect. The true canyon depth is at A.

flat floor is $\frac{1}{2}$ mile wide, then the actual width must be $\frac{1}{2}$ mile plus the radius of the effective cone of sound taken twice. This diameter can be calculated from the equation:

$$\begin{aligned} \text{depth plus echo length} &= \text{depth}/\cos \phi, \\ 1705 + 30 &= 1705/\cos \phi, \\ \phi &= 11^\circ 30'. \end{aligned}$$

Then by solving the right triangle the diameter of the effective cone at this depth and gain setting is 4,152 feet, making the true width of the canyon $1\frac{1}{4}$ miles. The canyon's walls slope at 6° with the horizontal. The slope of the southeast wall appears to be the same as that of the northwest wall, though the northwest rim is five fathoms higher, this discrepancy being due partly to the fact that the ship's track is up the continental rise. Downstream from this crossing the tributary turns south and thence southeast to run parallel with the main Hudson Canyon for about 100 miles with an average gradient of 40 feet per mile; it then joins the main Canyon at 2300 fathoms, where it may form one of the series of coalescing fans that build out the Hudson Canyon delta (4), (6).

That this tributary has a flat floor at 1705 fathoms while the main Hudson Canyon is V-shaped at 1715 fathoms may be due to the fact that the Hudson Canyon has a gradient of 60 feet per mile while tributary C has one of only 40 feet per mile. The tributary's lower

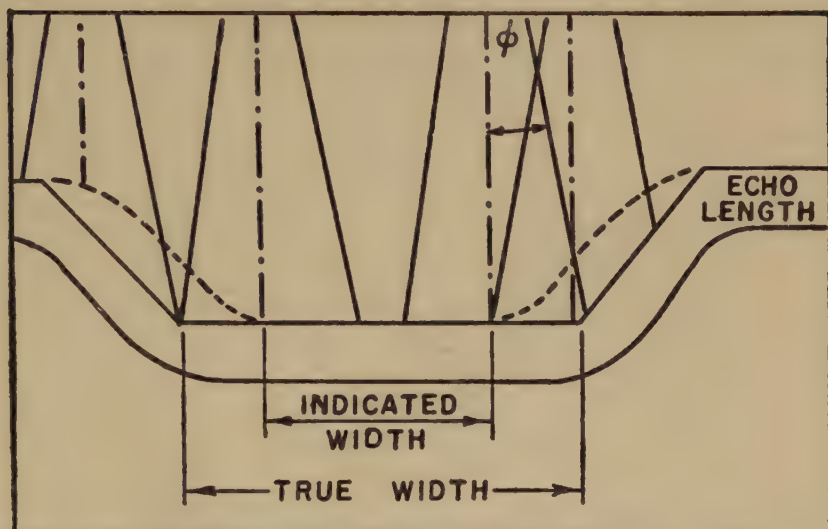


Figure 4. Indicated and true width of a flat-bottom canyon.

gradient is probably not sufficient to transport sands or gravel as in the main Canyon, where both arenites and lutites are transported out into deeper water, leaving only the larger pebbles behind. The capacity and eroding power of the turbidity currents coming down the main Canyon would be greater than those in the tributary because the turbidity currents in the former have a greater area in the upper reaches of the Canyon in which to gather material and momentum.

Tributary *D* (Figs. 1 and 2), also on the east side of the main Canyon, was crossed 11 miles further downslope from tributary *C*. The bottom of this tributary is 15 fathoms below the southeast bank and 30 fathoms below the northwest bank. In other words, the up-slope side is 15 fathoms higher, which indicates that the continental rise is steeper here than at *C*. However, this illusion may be caused by the fact that the ship's track was more normal to the regional contours in the former case.

It is difficult to compute the true shape of this canyon because the instrument's gain was increased after the cone of sound entered the canyon. Working with the record from where the gain was increased, the effective cone (by the equation) is 14° , which gives an effective base diameter of 4,484 feet. Inasmuch as the bottom of the styli markings shows a rounded contour compared to the V shape of the upper terminus, the width of the canyon is less than the effective

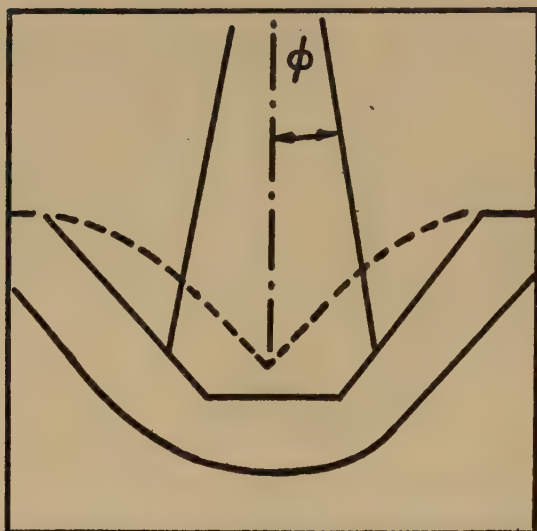


Figure 5. The rounded bottom edge of the echogram is due to the canyon's width being less than the diameter of the effective cone of sound.

diameter of the cone of sound and hence the true depth is greater than that shown (Fig. 5). No further computations can be attempted because of the change in gain setting of the instrument.

CONCLUSIONS

Although the Hudson Submarine Canyon can be traced headward to the continental shelf, its tributaries, like *B*, *C*, and *D* of this report, seem to stop short of the continental shelf. The Hudson Canyon has a deep V-shaped profile where it cuts into the continental rise while its major tributary canyon has a flat bottom. It may be that the main Canyon was better developed during a time of lower sea level than the tributaries, which have no *bona fide* parent river and which owe their shape to submarine slumping and turbidity currents alone. However, erosion by turbidity currents would be much greater in the main Canyon because it is a trunk stream, and any contributing turbidity currents would flow toward and then down the main Canyon, bypassing downstream tributary canyons. Thus the main Canyon would be the route of larger and more numerous currents and could be cut deeper. Turbidity currents can erode only the bottom of the Canyon. Material slumping down off the walls has modified the steepness of the Canyon walls and has started small tributaries, like *B* of this report, which are very short. As this process continues, a

tributary would elongate and encroach headward, although its channel might be filled with sediment left by weaker currents, as in tributary C of this report.

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MICROFILTRATION IN OCEANOGRAPHIC RESEARCH

II. RETENTION OF COLLOIDAL MICELLES BY ADSORPTIVE FILTERS AND BY FILTER-FEEDING INVERTEBRATES; PROPORTIONS OF DISPERSED ORGANIC TO DISPERSED INORGANIC MATTER AND TO ORGANIC SOLUTES¹

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ABSTRACT

To adsorb and retain quantitatively the minute colloidal micelles held in dilute suspensions, fine inert inorganic powders (such as MgO and refined diatomaceous earth) or finely porous cellulose membranes may be employed. Minute micelles, such as molecular hemoglobin, are retained also by setous or ciliary-mucous filter-feeders. Microfiltration is applicable in preparing bacteria-free aqueous filtrates and in determining the preponderance of organic *dispersoids* over organic *solutes* in natural waters. Molecular filter membranes have been used to demonstrate the high variability of total leptopel concentrations and to indicate the inconstancy of ratios between organic and inorganic dispersoids.

Current studies of marine biochemical cycles involve the use of adsorptive filters for the recovery, concentration and quantitative studies of leptopel, the finely particulate organic and inorganic matter suspended in water (Fox, Isaacs and Corcoran, 1952; Goldberg, Baker and Fox, 1952). Although careful experimentation indicated that marine hydrocolloidal micelles must be quantitatively retained either by adsorptive powder filters or by cellulose acetate and nitrate molecular filter (MF) membranes, it was necessary to resolve other critical questions, such as (a) the fineness of micelles retainable by such filters, (b) ratios between quantities of organic and inorganic leptopelic components, and (c) proportions between finely *particulate* and truly *dissolved* organic matter in the sea. These problems have involved (1) testing each type of filter for its retention of extremely small micelles of approximately known size, such as hemoglobins, (2)

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determining the total dry weight and ash weight of leptonel retained by ashless MF membranes, and (3) measuring the biochemical oxygen demand of endemic marine micro-organisms which utilize total organic matter in raw samples of sea water, comparing such measurements with determinations of the micro-organisms' use of dissolved molecules which remain in filtered samples. The removal of bacteria from sea water systems with each type of filter has also been confirmed (cf. Goetz and Tsuneishi, 1951; Clark and Kabler, 1952).

RETENTION OF COLLOIDAL MICELLES BY ADSORPTIVE FILTERS

Substances Tested and Their Properties

(a) Oxyhemoglobin from a tide-pool blenny (not specifically identified) and from the marine goby *Gillichthys mirabilis*; micellar size of vertebrate hemoglobins = ca 50 Å (McBain, 1950: 128); molecular weight, ca 70,000.

(b) Oxyhemoglobin from the marine polychaete worm *Thoracophelia mucronata*; micellar size two- to ten-fold that of the fish hemoglobin as estimated by ultramicroscopic (dark-field cardioid condenser) examination of both species. Suspensions of about 2 ppm were used in experiments.

Filters and Reagents

(a) Adsorptive powder filters: equal parts of finely powdered MgO (reagent grade) and pure SiO₂ as "Super-cel," a refined diatomaceous earth (Fox, Isaacs and Corcoran, 1952).

(b) Molecular filter (MF) membranes of finely porous cellulose acetate-nitrate (Goldberg, Baker and Fox, 1952).

(c) Freshly prepared (or carefully preserved and always pretested) solutions of benzidine in equivalent parts of glacial acetic acid and hydrogen peroxide (Hawk, Oser and Summerson, 1947).

(d) Special adsorptive refiltering medium consisting of 5 parts Super-cel and 1 part Ca(OH)₂ to retain hemoglobin quantitatively from suspensions of 1 part or less in 10⁸. This medium, less active than MgO in gradually catalyzing the decomposition of H₂O₂ to yield a "blank" blue color reaction with benzidine, is used for reprocessing filtrates from the other microfiltrational devices. Traces of hemoglobin, retained in suspensions too dilute to yield a positive benzidine reaction on a direct test of the filtrate, are readily detected by passing the fluid through the thin powder pad and by finally applying the test directly to the pad's damp upper surface where any traces of residual hemoglobin would have been concentrated. Powders containing Ca(OH)₂ are more effective with sea water than with distilled or

fresh water, since, in the former medium, the sparingly soluble base immediately precipitates gelatinous flocks of insoluble and strongly adsorbent $\text{Mg}(\text{OH})_2$.

Precautions

(a) Adsorptive powder-filter suspensions should be allowed to settle for a few minutes in the porous cup, should be firmly packed into position by initial suction before using, and should remain covered with water at all times in order to preclude the formation of cracks or other channels.

(b) Use of excessive amounts of $\text{Ca}(\text{OH})_2$ should be avoided in the filtration of sea water systems, since any considerable proportions of the resulting $\text{Mg}(\text{OH})_2$ precipitate tend to clog the filter.

(c) An excess of the neutral adsorbent must be present, since this filtrational process is one of *adsorption* rather than mere physical screening. Hence a given quantity or surface area of the adsorbent will possess a limiting saturation value which, if exceeded by the concentration of the adsorbate (e. g. hemoglobin), will allow micelles of the latter to pass.

(d) Numerous types of surface, including the finely powdered MgO -Super-cel mixture, catalyze the decomposition of H_2O_2 , thus yielding free O_2 which reacts with benzidine. However, the blue color thus produced appears rather slowly in contrast with the instantaneous manifestation of green or blue-green colors produced by adsorbed hemoglobin. Moreover, this "blank" blue reaction is still more retarded when $\text{Ca}(\text{OH})_2$ has been substituted for MgO as a sea water filter. If these factors are kept in mind, there is no difficulty in recognizing the presence of adsorbed hemoglobin.

Results. Four-liter suspensions of fish hemoglobin that had been separated from the laked corpuscular envelopes, and of worm hemoglobin, were resolved by filtration through adsorptive powder columns [0.5 g MgO ; 0.5 g Super-cel, and optionally 0.1 g $\text{Ca}(\text{OH})_2$] of about 4 mm thickness. Hemoglobin concentrations of 2 ppm or 8 mg total were used in both sea water and distilled water. Following the operation, the damp filter-cake was removed and the benzidine test was applied. Its top surface responded positively at once while the bottom surface was negative; cross sections of the fractured cake showed that the hemoglobin was adsorbed in the upper 1 to 2 mm; its quantitative adsorption was clearly indicated by a distinct color boundary part way through the cake. Complete removal of the hemoglobin was further confirmed by passing the filtrate from the first operation through a second adsorptive powder-cake of 5 parts

Super-cel and 1 part $\text{Ca}(\text{OH})_2$; application of the benzidine test to its damp top surface gave negative results. Molecular filter membranes of different porosities were likewise employed for processing similar volumes of dilute, laked and cleared hemoglobin suspensions in sea water and in distilled water. The resulting filtrates were then tested for residual hemoglobin by using the Super-cel- $\text{Ca}(\text{OH})_2$ powder as above.

The following filter membranes which were used are designated by their Z-number (time in seconds required for 1 ml of water to pass through 1 cm^2 of surface area at 700 mm pressure) and their VC value (volume ratio of cellulose material to air space).

Filter No.	Z No.	V C	Hemoglobin in distilled water	Hemoglobin in sea water
5001-12	0.035		Passed	Passed
1152-6	0.26	0.142	Passed	Passed
2010	1.0	0.200	Sometimes passed little*	Sometimes passed traces*
1122-5	2.6	0.213	Sometimes passed little*	Sometimes passed traces*
1122-3	8.0	0.249	—	Retained all
1152-8	20.0	0.269	Retained all	Retained all

* We believe that in some instances adventitious soluble heme degradation products might have passed through the filter, since heme crystals dissolved in water give a strong reaction with benzidine. Furthermore, while the test failed at a dilution of 1 : 25,000, it responded after the heme from this solution had been retained on a Super-cel + $\text{Ca}(\text{OH})_2$ filter

From the foregoing experiments it is concluded that the MgO + Super-cel adsorptive powder, as well as cellulose filters of fine porosities, will quantitatively adsorb extremely fine micelles (such as vertebrate hemoglobin) from very attenuated suspensions, and that such micro-filtrational operations are therefore suitable for the quantitative resolution of marine colloids. Indeed, most marine colloidal micelles are probably of much larger mean diameter than hemoglobin, and, in view of the presence of the divalent cations and charged micelles, they must occur in various degrees of adsorption, agglomeration or coacervation.

RETENTION OF DISPERSED HEMOGLOBIN BY FILTER-FEEDING INVERTEBRATES

Because our chief interest was concerned with the fineness of colloidal micelles which may be removed by filter-feeders, we conducted a few experiments on the retention of molecularly dispersed fish hemoglobin by two different and widely distributed marine

invertebrates: a mysid crustacean (not specifically identified) which was collected in the vicinity of kelp beds and slicks off La Jolla; the sea mussel, *Mytilus californianus*, which grows in large numbers and is attached to intertidally exposed rocks and pier pilings.

Both control and experimental mysids were placed in previously microfiltered sea water. A small volume of laked and paper-filtered hemoglobin was then added to the microfiltered water that contained the experimentals, which, in contrast with the controls, conspicuously manifested the full dark-colored contents of their alimentary tracts. In numerous instances they had next day voided long dark rod-like fecal strands, which, upon microscopic inspection, especially after mashing under a cover glass, showed green or blue responses to the benzidine test, thus indicating the presence of heme or hemoglobin.

Similarly, both the pseudofeces and stomach rinsings of mussels exposed to dilute molecularly dispersed hemoglobin yielded green colors with benzidine while those of the control animals were negative in this regard. Likewise, the white experimentally talc-laden feces of mussels which had previously received hemoglobin exhibited purple colors with benzidine as well as positive tests for iron in the presence of thiocyanate.

These experiments are regarded as demonstrative of the ability of two representative filter-feeders (one setous, the other ciliary and mucous) to adsorb from suspension colloidal particles of such extremely fine dimensions as those of vertebrate oxyhemoglobin, i. e., 40 to 50 Å. Microfiltrational operations with adsorptive powders or molecular filters may be used to recover the dispersed phases of natural hydrosols, including colloiddally dispersed materials commonly gathered by mucous or other filter-feeding aquatic animals.

PROPORTION BETWEEN ORGANIC AND INORGANIC LEPTOPELIC CONSTITUENTS

Goldberg, Baker and Fox (1952) have demonstrated in duplicate samples and with respect to depth the wide variability of finely particulate inorganic matter in the sea, while Fox, Isaacs and Corcoran (1952) have supplied similar information pertaining to organic leptopel. The inhomogeneity of these materials, their changing concentrations with time, and the variability in ratio between organic and inorganic leptopel, were confirmed with the molecular filter in two additional experiments reported here.

Two 4-liter samples, collected in relatively nonwetttable polyethylene bottles, were taken from about 20 feet beneath the surface at the end of the Scripps Institution's pier, 1,000 feet offshore. Sample I was

collected during a period of high surf, when the offshore waters contained much visible suspended matter; sample II was taken on the following day when the sea had subsided to a normal surf and when the water was less turbid. In the laboratory, the coarser particles of sand and mica settled out of suspension, and floating algal fragments were removed from the water surface.

Each 4-liter sample was passed through an ashless cellulose membrane filter ($Z = 2.6$). The residue was leached *in situ* with distilled water, and the membrane, with its retained particulate material, was then dried at 80° C for six hours in a vacuum oven. After weighing, each membrane was ignited, and the ash weight was recorded as follows:

		Ash	Organic matter	Organic
	Total dry solids (mg/L)	(mg/L)	by difference (mg/L)	Matter (%)
Sample I	10.5	4.0	6.5	62
Sample II	3.8	2.7	1.1	29

These two random samples thus exhibit nearly a three-fold variation in total leptonel content and more than a two-fold difference in the proportion of the organic component.

The value of 29% organic matter obtained from Sample II is close to the figure obtained previously for solid material collected from a marine slick (27%; Fox, Isaacs and Corcoran, 1952) and to the figure derived from several analyses of the flocculent portions of feces from a typical detritus filterer, the California mussel (31%; Fox and Coe, 1943).

PROPORTIONS BETWEEN DISPERSED AND DISSOLVED ORGANIC MATTER IN SEA WATER

Method. Samples of raw sea water were freshly collected in clean and relatively nonwetttable plastic bottles. The untreated sea water and filtrates derived from it were assayed for their respective content of (a) original dispersed and dissolved organic matter combined, and (b) organic solutes by determining (with the Winkler method) the biochemical oxygen demand (B. O. D.) of multiple aliquots. The raw sea water already contained a normal flora of micro-organisms and was therefore ready for incubation. However, each of the filtered samples was inoculated with 5 ml raw sea water per liter in order to provide mixed populations of marine bacteria. This inoculation supplemented the organic matter by no more than 0.5% of the original supply. The multiple aliquots, incubated at 27 to 28° C in 60-ml glass-stoppered bottles, were analyzed for residual dissolved oxygen before incubation and at specified intervals (Figs. 1, 2, 3).

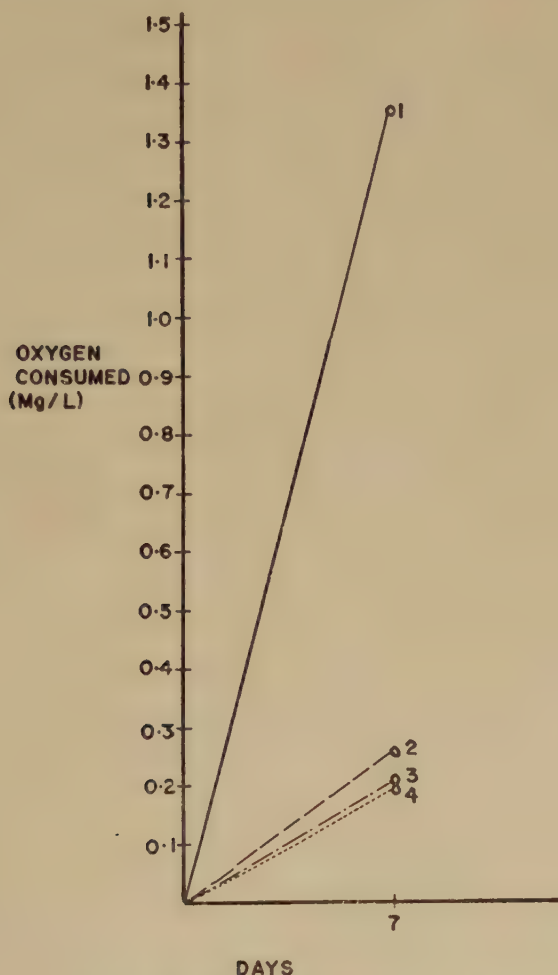


Figure 1. B. O. D. of sea water: (1) raw and untreated; (2) after powder treatment and paper filtration; (3) after powder filtration; (4) after MF filtration. Incubation temperature, 28° C; ratio between retained and filter-passing organic matter (7 days' incubation): ca 85 : 15%.

Results. Experiment I. Paired samples of sea water were incubated in the following stages: (1) in the raw state, (2) after occasional shaking with a little powdered MgO during a two-hour period and subsequent filtering by gravity through a superimposed pair of No. 50 Whatman filter paper cones, (3) following filtration by suction through a packed column of adsorptive powder (equal weights of MgO and

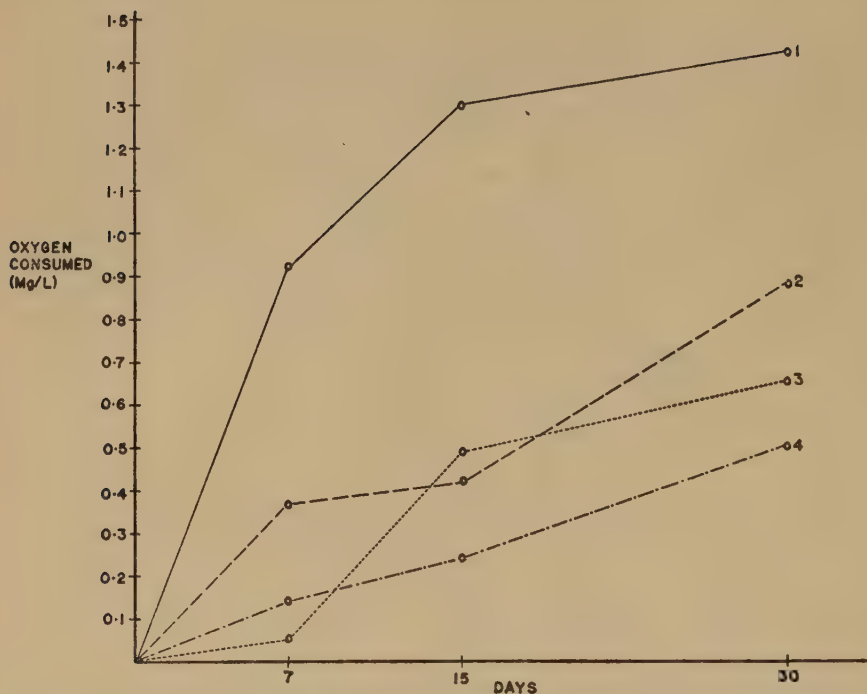


Figure 2. B. O. D. of sea water: (1) raw and untreated; (2) after powder treatment and paper filtration; (3) after powder filtration; (4) after MF filtration. Incubation temperature, 27° C; ratio between retained and filter-passing organic matter (i. e. comparing B. O. D. of curve 1 with the average values of curves 3 and 4 after 30 days): ca 60 : 40 %.

Super-cel), and (4) after passage through a fine MF membrane ($Z = 8.5$). B. O. D. measurements were made after culturing for seven days at 28° C; the results are plotted in Fig. 1.

Experiment II. The above experiment was repeated with fresh sea water and with measurements of the B. O. D. of quadruplicate or triplicate aliquot samples after incubation for 7, 15 and 30 days at 27° C. Values for the average quantities of oxygen consumed are plotted in Fig. 2.

Experiment III. Since the rubber connections used in the assembly which employed adsorptive powder might have contributed traces of contaminating organic material to the filtrates, comparisons were made between the B. O. D. of sea water (1) before it was treated and (2) after it was filtered through the adsorptive powder in a Morton filter apparatus, which is constructed entirely of glass, i. e., with ground joint and a fine sintered glass disc that is capable of retaining

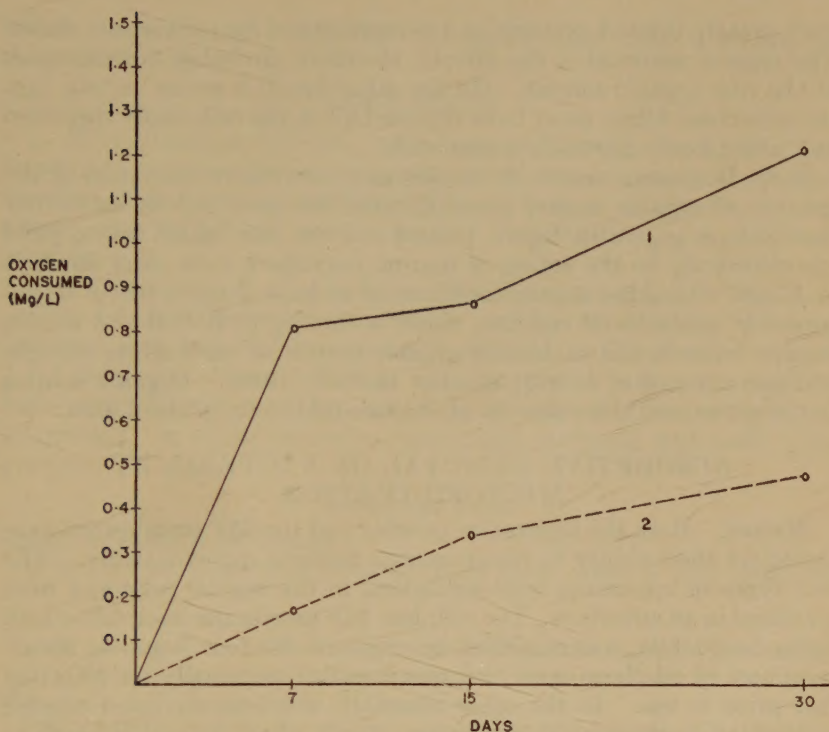


Figure 3. B. O. D. of sea water: (1) raw and untreated; (2) after powder filtration in all-glass Morton apparatus. Incubation temperature, 27° C; ratio between retained and filter-passing organic matter (30 days' incubation): ca 61 : 39%.

bacteria in filtrational sterilization of media. Before use, the whole apparatus was dismantled, its parts were treated separately with hot concentrated nitric or hot concentrated chromic and sulphuric acids, and all parts were ultimately rinsed free of acid with twice-distilled water. Average values of B. O. D. measurements, made on multiple aliquot samples of each medium after incubation for 7, 15 and 30 days at 27° C, are plotted in Fig. 3. Close agreement between the data in experiments II and III suggests that the former involved no contaminants.

From a study of the graphs it is apparent that the major proportion ($\frac{3}{5}$ or more) of the organic matter in sea water existed in a colloidal or other particulate state rather than in the dissolved condition. While traces of some organic solutes may be adsorbed by the powder or by the cellulose material of the molecular filter, it is highly improbable that such adsorption occurs to a significant extent, especially from

such greatly diluted systems as are represented by normal sea water. The organic material in the filtrate, therefore, probably represents all of the true organic solutes. On the other hand, it seems certain that the adsorbent filters must have retained all of the colloiddally dispersed and other finely particulate material.

B. O. D. measurements serve only as conservative indicators of the amount of organic matter present, since this may include refractory materials, e. g., chitin, lignin, humus and the like, which fail to yield quantitatively to the action of marine microflora even after 30 days at 27–28° C. Also, organic residues of at least 2 parts in 10⁷ would probably apply to all cultures, since, according to ZoBell and Grant, marine bacteria fail to destroy organic matter at such dilute concentrations even after several months (ZoBell, 1946). Organic solutes in the sea exceed this value by about two-fold in the plotted data.

ADSORPTIVE REMOVAL OF BACTERIA BY MICROFILTRATION

Method. Both the adsorptive powder and the MF membranes were tested for their ability to retain marine bacteria quantitatively. The two types of apparatus were assembled in the regular way and were sterilized in an autoclave. The cellulose MF membrane itself ($Z = 1.4$), being heat-labile, was sterilized by exposure for four hours to an atmosphere of ethylene oxide and was installed aseptically for filtration just prior to use. In the other assembly, the heat-sterilized powder was added to the special sterile cup; sterile water, passed through to seat the powder pad, was received in a sterile test tube which was ultimately removed before the main operation.

Raw sea water, containing approximately 1,000 bacteria per ml, was processed through each filter. Filtrate samples 1 ml in volume were transferred to a series of tubes, each of which contained 5 ml of sterile nutrient sea-water broth (ZoBell, 1946: 41); incubation was then carried out at 27° C.

Results. After 72 hours of incubation, all tubes remained sterile. They were therefore inoculated with mixed marine bacteria to determine whether the filtrate had perchance contained any antibacterial contaminants. After reincubation at 27° C for 24 hours, the contents of all tubes were distinctly turbid, indicating bacterial growth.

It was concluded, therefore, that each type of filter is capable of removing all bacteria from sea water without destroying its ability to support bacterial multiplication. Bacterially sterile and leptopel-free sea water, ionically balanced and of low residual organic (solute) content, may be readily prepared for media or other purposes by

aseptic microfiltration followed by equilibration with a stream of sterile filtered air.

SUMMARY

1. Microfiltration with fine, inert inorganic powders (e. g., MgO + Super-cel) or fine cellulose membranes will retain very fine colloidal micelles, such as molecular hemoglobin, which is adsorbable also by setous and by ciliary mucous-feeding animals (e. g., mysids and mussels).

2. The same types of adsorptive filters are also applicable in preparing bacteria-free aqueous filtrates and in determining the preponderance of *dispersed* over *dissolved* organic matter in natural waters.

3. Molecular filter membranes have been used to demonstrate the high variability of total leptopel concentrations and to indicate the inconstancy of ratios between organic and inorganic leptopelic components.

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